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ZOOGEOGRAPHIC AND EVOLUTIONARY RELATIONSHIPS OF SELECTED POPULATIONS OF MICROTUS MEXICANUS

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Upper elevations of the higher mountains of the southwestern United States are inhabited by several species of boreal mammals that have been isolated on these mountain refugia for varying periods of time. These restricted populations provide an opportunity for investigating zoogeographic and evolutionary principles. One such mammal, the Mexican vole (*Microtus mexicanus*), chosen as the basis of this study, presently inhabits the Transition Zone on scattered mountain ranges from southwestern Colorado to the Mexican state of Veracruz. It typically is found in dry bunchgrass meadows and mesic grasslands scattered among yellow pine and fir at elevations generally above 2000 meters (m.). *M. mexicanus* is more tolerant of xeric conditions than are other microtines inhabiting this area and is often found considerable distances from any source of permanent water (Findley and Jones, 1962). The isolated nature of mountains in the Southwest and relatively small geographic ranges of the species have resulted in a series of small, isolated *Microtus mexicanus* populations.

This study concerns four populations of the Mexican vole located in the San Mateo, Manzano, Sacramento, and Guadalupe mountain ranges of New Mexico and Texas. These mountain ranges are separated from one another by variable expanses of dry lowlands, generally consisting of unsuitable habitat for microtine rodents. Three of the four populations have been referred previously to the subspecies *M. m. guadalupensis* (Manzano, Sacramento, and Guadalupe mountain populations); the remaining San Mateo Mountain population was referred to *M. m. mogollonensis* (Hall and Kelson, 1959).

The primary objectives of this investigation were to reevaluate present subspecific assignments of populations of *M. mexicanus* in the region of study, to compare conclusions obtained by means of classical taxonomic methods with those obtained by using more recent systematic methods, to examine the zoogeographic history and evolutionary relationships of the populations concerned, and to attempt to place the evolutionary changes observed into a reasonable temporal framework. Additionally, this investigation was intended to explore aspects of the biology of *M. mexicanus* that previously have not been covered in the literature. These four populations of the Mexican vole were examined using protein electrophoresis, karyotypic analysis, sperm morphology, bacular morphology, and classical morphometrics.

METHODS AND MATERIALS

Mexican voles were captured in Sherman live traps during the months indicated at the following localities: TEXAS: Culberson Co.: Upper Dog Canyon, Guadalupe Mountains National Park (April, August, December); The Bowl, Guadalupe Mountains National Park (August). NEW MEXICO: Torrance Co.: 4th of July Campground, Cibola National Forest (September, October); Lincoln Co.: South Fork Campground, Lincoln National Forest (May, October, November); Soccoro Co.: Beartrap Canyon, Cibola National Forest (October). The collecting localities and the extent of the mountain ranges involved are illustrated in Fig. 1.

After collection, voles were transported from the field to the laboratory and were usually sacrificed within two weeks of capture. A total of 379 specimens of *M. mexicanus* were examined, including 121 that were live trapped and maintained in the laboratory for varying periods before being killed. All were prepared as standard museum skins and skulls and deposited in The Museum, Texas Tech University.

Karyotypes were prepared following the *in vivo* technique of Baker (1970). A minimum of five metaphase spreads were counted for each of 42 males and 49 females examined. Terminology describing chromosomal morphology and fundamental number follows that of Patton (1967).

Spermatozoa were obtained by removing the epididymis from freshly killed specimens, mincing it with scissors, and suspending

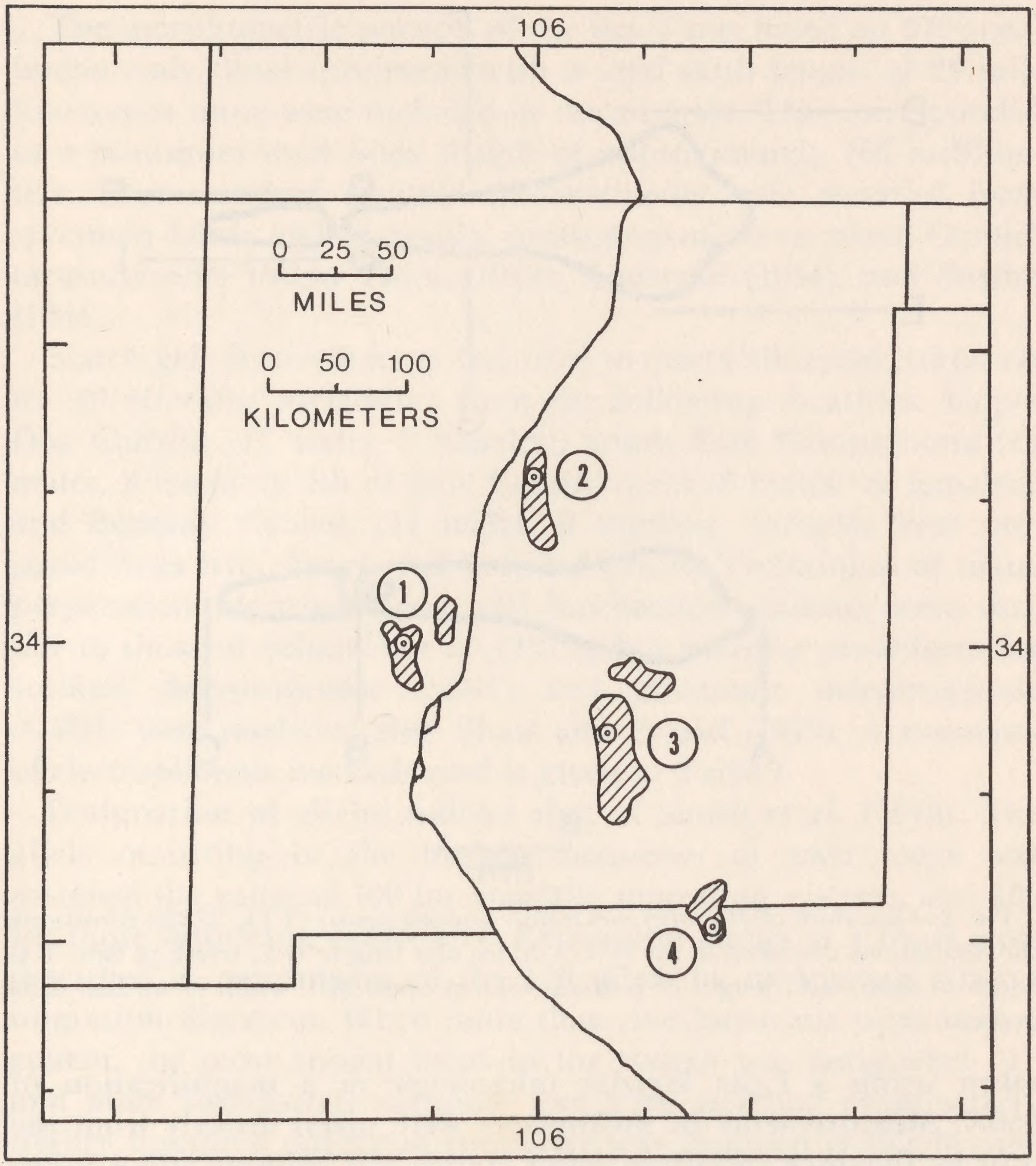

FIG. 1.—Geographic relationships and approximate extent of the mountain ranges containing collecting localities for populations of *Microtus mexicanus* examined. Localities are identified by numbers: 1) Beartrap Canyon (San Mateo Mountains, Soccoro County, New Mexico); 2) 4th of July Campground (Manzano Mountains, Torrance County, New Mexico); 3) South Fork Campground (Sacramento Mountains, Lincoln County, New Mexico); 4) Guadalupe Mountains (Culberson County, Texas). Circles indicate approximate collecting localities within each mountain range.

a small amount of fluid from the minced tissue in an isotonic solution of sodium citrate. Several drops of this solution were placed on a microscope slide and allowed to air dry. Slides were then fixed in a solution of one part acetic acid and four parts methanol prior to staining with a 0.15 per cent solution of Giemsa in hot water. Photomicrographs of spermatozoa were

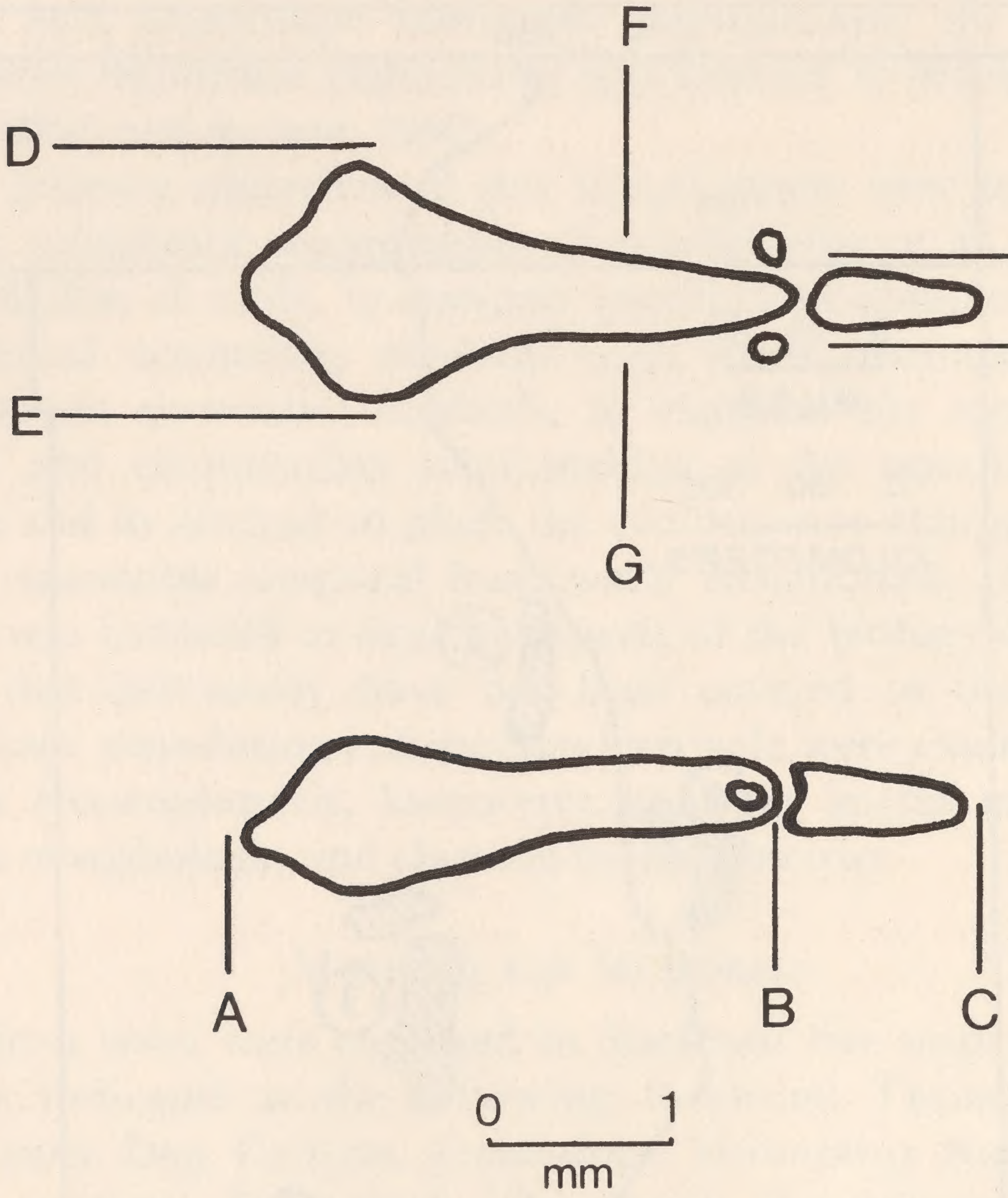

FIG. 2.—Baculum of *Microtus mexicanus guadalupensis* (TTU 27326) illustrating the dimensions described in the text: A-B, bacular length; D-E, width of base; F-G, width of shaft; B-C, length of median distal process; H-I, width of median distal process.

taken using a Leitz Wetzlar microscope at a magnification of 950×. Measurements in millimeters were taken directly from the four by five-inch negatives using Helios dial calipers and a Sakurai map measuring device. Measurements and terminology follow those of Linzey and Layne (1974). Ten spermatozoa were measured for each of the 28 specimens examined, and average values were used in the subsequent analyses.

Penes were removed from freshly killed specimens and stored in AFA; bacular preparation followed techniques outlined by Anderson (1960). After staining and destaining, penes were dissected away from the bacula, and the bacula were drawn in both dorsal and lateral views using a camera lucida attached to a Wild M5 microscope at a magnification of 12×. Measurements (in millimeters) of 64 specimens were taken directly from the drawings and included: bacular length, width at base, width of shaft, length of median distal process, and width of median distal process when an ossified distal process was present (Fig. 2).

The morphometric portion of the study was based on 379 specimens; only those specimens with a total skull length of 23 millimeters or more were included in the analysis. This corresponded to a minimum total body length of approximately 100 millimeters. Four standard external measurements were recorded from specimen labels and 14 cranial measurements were taken. Cranial measurements follow Goin (1943), Anderson (1954), and Snyder (1954).

Starch gel electrophoresis was used to assess allozymic variation for 80 *Microtus mexicanus* from the following localities: Upper Dog Canyon (11 males, 9 females); South Fork Campground (12 males, 8 females); 4th of July Campground (8 males, 12 females); and Beartrap Canyon (11 males, 9 females). Samples were prepared from liver, heart, and kidney extracts. Techniques of tissue preparation, electrophoresis, and biochemical staining were similar to those of Selander *et al.* (1971), but staining procedures for sorbitol dehydrogenase (SDH) and glutamate dehydrogenase (GDH) were modified after Shaw and Prasad (1970). A summary of electrophoretic methods used is given in Table 1.

Designation of alleles follows that of Smith *et al.* (1973). The allele occurring in the highest frequency at each locus was assigned the value of 100 for anodally migrating systems, or −100 for those migrating cathodally. Remaining alleles at a locus were described as percentages of the 100 allele by comparing relative migration distances. When more than one locus was present in a system, the most anodal locus in the system was designated "1" and more successively cathodal loci were assigned progressively higher numbers. Allozyme similarity was assumed if side-by-side comparisons failed to establish differences (see Smith *et al.*, 1973).

Statistical and clustering analyses were carried out using SAS·76 (Barr *et al.*, 1976), UNIVAR (Power, 1970), and NT-SYS programs. In all analyses, specimens were grouped into four aggregate populations representing the primary collecting localities; these aggregates were considered as Operational Taxonomic Units (OTU's).

SAS programs were used in univariate analyses to provide standard descriptive statistics and to perform both single classification and two-way analyses of variance in order to test for significant differences between or among means. When means were found to be significantly different, the Sums of Squares Simultaneous Test Procedure (SS-STP) was conducted using a UNIVAR program to determine maximally nonsignificant subsets. Multivariate analyses entailed calculation of Pearson product-moment correlation coefficients, again using SAS, to compare electrophoretic distance and correlation matrices with the corresponding morphometric and sperm morphology matrices. Cluster analyses were conducted on the correlation and distance matrices and a two-dimensional phenogram was generated for each using the NT-SYS program. This program utilizes the unweighted pair-group method using arithmetic averages (UPGMA). Phenograms were compared with their respective matrices and a coefficient of cophenetic correlation was computed for each comparison to assess the reliability of the phenogram. A matrix of correlation among the characters was computed, and the first principal components were extracted. A three-dimensional plot of the OTU's onto the first three principal components was then prepared. The percentage of the total variation accounted for by each principal component was calculated, as was the contribution of each character to each of the principal components. Additional data concerning methods and materials may be found in Wilhelm (1977).

Specimens Examined

In addition to specimens collected for this study, other specimens were borrowed from the following institutions for examination: Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); The Museum, Texas Tech University (TTU); University of New Mexico (UNM); and University of Texas at El Paso (UTEP). Localities are not plotted separately on Fig. 1, but are grouped with the four primary collecting sites for purposes of analysis and discussion. The list below includes all specimens examined.

Microtus mexicanus guadalupensis (300).—Texas: *Culberson County*: Guadalupe Mountains National Park, The Bowl, 24 (6 TTU, 18 TCWC); Upper Dog Canyon, 33 (TTU); Guadalupe Peak, 1 (TTU). New Mexico: *Otero County*: Timberon, 2 (TTU); 8.5 mi. E, 4.5 mi. N Almo Peak, 2 (UNM); 1 mi. N Cloudcroft, 2 (UNM); 7 mi. E Cloudcroft, 2 (UNM); 7 mi. E, 2.5 mi. N Cloudcroft, 7 (UNM); 1 mi. S Cloudcroft, 1 (UNM); 10 mi. S Cloudcroft, 15 (UNM); 2 mi. W Cloudcroft, 1 (UNM); 2.4 mi. W Cloudcroft, 1 (UTEP); near Cloudcroft, 19 (8 UTEP, 11 TTU); Russian Canyon, 5 mi. S, 2.5 mi. E Cloudcroft, 2 (UTEP); north of Ruidoso, 3 (UTEP). *Lincoln County:* Padilla Point, 3 (UTEP); South Fork Campground, 27 (TTU); 5 mi. N, 9 mi. E Capitan, 2 (UNM); 1.5 mi. W Capitan, 3 (UNM); Capitan Mountains, 20 (UNM); Monjeau Peak, 10,000 ft., 6 (UNM); Lincoln County, 6 (TTU). *Torrance County*: 4th of July Campground, 36 (TTU); 0.5 mi. S Capillo Peak, 9000 ft., 1 (UNM); 5.5 mi. W Tajique, 8 (UNM); Red Canyon, 0.5 mi. S, 5 mi. W. Manzano, 34 (UNM); Red Canyon, 4 mi. W, 1 mi. S Manzano, 11 (UNM); 5 mi. W Manzano, 3 (UNM); Torrance County, 4 (TTU). *Bernalillo County*: Tree Springs, 8600 ft., 21 (UNM).

TABLE 1.—*Electrophoretic techniques utilized in this study. All gels were run for five hours.*

Gel type	tissue	milliamperage	stains
1. Continuous Tris-citrate I	Kidney	75	Lactate dehydrogenase (LDH)
	Kidney	75	Malate dehydrogenase (MDH)
	Kidney	75	Malate enzyme (ME)
	Kidney	75	Isocitrate dehydrogenase (IDH)
	Kidney	75	Acid phosphatase (ACP)
2. Continuous Tris-citrate II	Liver	85	Sorbitol dehydrogenase (SDH)
	Liver	85	Alcohol dehydrogenase (ADH)
	Liver	85	Glutamate oxalate transaminase (GOT)
	Liver	75	Leucine aminopeptidase (LAP)
3. Lithium Hydroxide	Kidney	80	Phosphoglucose isomerase (PGI)
	Kidney	90	Albumin (AB)
	Liver	75	Esterases (EST)
4. Phosphate	Liver	75	Phosphoglucomutase (PGM)
5. Discontinuous Tris-citrate (Poulik)	Kidney	85	Glucose-6-phosphate dehydrogenase (G-6-P)
	Kidney	85	Indophenol oxidase (IPO)
	Kidney	85	Alkaline phosphatase (AKP)
	Kidney	85	Xanthine dehydrogenase (XDH)
6. Tris-versene-borate	Kidney	85	Glutamate dehydrogenase (GDH)
	Kidney	85	αGlycerophosphate dehydrogenase (αGPDH)

Microtus mexicanus mogollonensis (79)—New Mexico: *Socorro County*: Beartrap Canyon, 78 (46 TTU, 28 UNM, 4 UTEP); 1.6 mi. from Water Canyon, 1 (UTEP).

Results and Discussion

Karyology

The karyotype of *Microtus mexicanus* was described from a single female specimen by Matthey (1957), who established the diploid number as 44. Being unable to identify the sex chromosomes, he was uncertain of the fundamental number and listed it as a minimum of 54 and perhaps 56.

The karyotype of *Microtus mexicanus* given in Fig. 3 shows a diploid number of 44 and a fundamental number of 54. No chromosomal polymorphism was noted among specimens examined. The autosomes consist of three pairs of large submetacentrics, one pair of medium submetacentrics, two pairs of small metacentrics, one pair of large acrocentrics, and 14 pairs of small acrocentrics. The X chromosome is a medium-sized submetacentric, and the Y is a small acrocentric.

Although no chromosomal polymorphism was found in the karyotype of the Mexican vole in this study, two separate chromosomal polymorphisms were described in Mexican voles from the states of Jalisco and Durango in México (Lee and Elder, 1977), and involved differences in both the diploid and fundamental numbers. Thus, *M. mexicanus* is the only exclusively Nearctic species of microtine from which infraspecific differences in chromosome morphology or number have been reported.

b Infraspecific variation in chromosome number is more common in Palearctic representatives of the genus, however. *Microtus hyperboreus* and *M. middendorfi* (Gileva, 1972) and *M. juldaschi* (Bol'shakov *et al.*, 1975) have been reported as polymorphic. Other genera of microtines that exhibit chromosomal polymorphism include *Dicrostonyx torquatus* (Rausch and Rausch, 1972; Kozlovskii, 1974), *Clethrionomys rutilus* (Rausch and Rausch, 1975), and *Pitimys subterraneus* (Meylan, 1972). The relatively few number of karyotypic studies of Nearctic microtines and the apparent uniformity of infraspecific chromosome complements might reflect a lack of data rather than extreme chromosomal conservatism of the group.

Sperm Morphology

Spermatozoa of *M. mexicanus* from the four populations studied were similar in all respects. The sperm head, widest just above

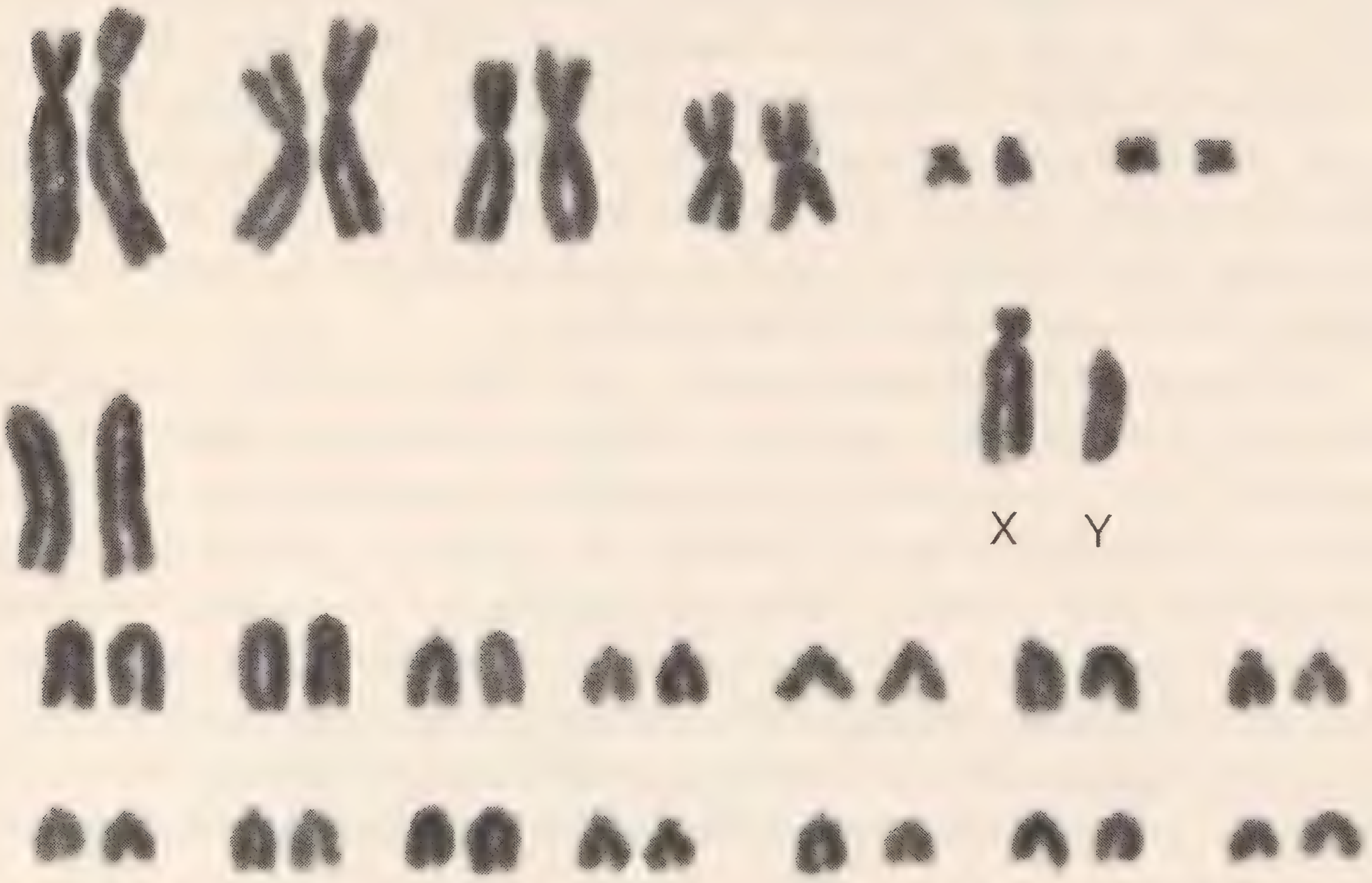

FIG. 3.—Karyotype of a male (TTU 27356) *Microtus mexicanus guadalupensis.*

the base, is asymmetrical with one margin convex and the other nearly straight. The base is smoothly convex with a notch on one side. Almost one-half of the head is enveloped by the acrosome, which is elongated into a recurved hook that lies on the side of the head having the straighter margin. Attachment of the midpiece is to the basal notch and is therefore eccentric. The tailpiece tapers gradually toward the tip and is sometimes difficult to distinguish from the midpiece. However, with the staining procedure used in this study, the tailpiece is generally of uniform appearance, whereas the midpiece is nearly always granular or mottled in appearance.

Mean values, followed by range in parentheses and sample size, for selected sperm measurements of *Microtus mexicanus* follow (measurements are in microns and localities are given in the order Beartrap, 4th of July, South Fork, and Guadalupe): *length of head,* 7.77(7.44-8.00) 5, 8.02(7.51-8.54) 5, 8.34(7.60-9.14) 10, 8.32(8.01-8.78) 8; *width of head,* 4.86(4.82-4.93) 5, 4.82(4.47-5.35) 5, 5.08(4.54-5.35) 10, 5.04(4.81-5.35) 8; *length of midpiece,* 18.45(17.12-20.32) 5, 18.10(16.80-18.80) 5, 18.32(16.72-19.36) 10, 18.46(15.84-20.72) 8; *length of tailpiece,* 66.02(60.16-71.36) 5, 70.21(65.84-74.32) 5, 72.02(68.48-76.08) 10, 70.51(65.92-73.04) 8.

Univariate analysis of sperm data showed a significant difference in the head width of spermatozoa ($P<0.05$) between some localities and in the length of the tailpiece ($P<0.01$) between others. The following nonsignificant subsets were generated by SS-STP tests: *width of head*—Guadalupe, 4th of July, Beartrap; *length of tailpiece*—South Fork, Guadalupe, 4th of July; Guadalupe, 4th of July, Beartrap. In *M. m. mogollonensis*, the sperm head is slightly shorter but just as broad as that of *M. m. guadalupensis*. The tailpiece of *M. m. mogollonensis* is considerably shorter than that of the other subspecies.

The four sperm measurements also were analyzed using the NT-SYS multivariate program. Both correlation and distance matrices were computed and phenograms representing the phenetic relationships were plotted. A Pearson product-moment correlation matrix was computed comparing these two matrices with the corresponding electrophoretic matrices. Correlation coefficients for neither the distance matrices nor the correlation matrices were significant. The distance phenogram showed that the Beartrap and 4th of July specimens had smaller sperm than did those from the other two localities. Although on the basis of sperm data, the Beartrap (*M. m. mogollonensis*) and the 4th of July (*M. m. guadalupensis*) populations more closely resembled each other than either resembled the other two populations, their relationship to each other was not of the same magnitude as was that of populations from the South Fork and Guadalupe localities.

In the principal components analysis, the amount of phenetic variation expressed in the first principal component was 65.58; in the second, 33.60; and in the third, 0.80. The percentage contribution of each sperm character to each principal component, given in the order Component I, II, and III were *length of head*, 10.51, 0.71, 32.05; *width of head*, 5.87, 3.81, 22.89; *length of tailpiece*, 81.70, 59.85, 7.38; *length of midpiece*, 1.91, 35.62, 37.65. Length of tailpiece accounts for most of the phenetic variation. A three-dimensional perspective of the projection of the four OTU's onto the first three components, based on a matrix of correlation among the four sperm measurements, is given in Fig. 4. Essentially the same pattern was seen in the distance phenogram. South Fork and Guadalupe OTU's were clustered close to one another; Beartrap and 4th of July OTU's were loosely grouped. This grouping of the populations sampled agreed in part with the results from multivariate analyses of cranial morphometric data. Small sample sizes, however, render these results of limited value.

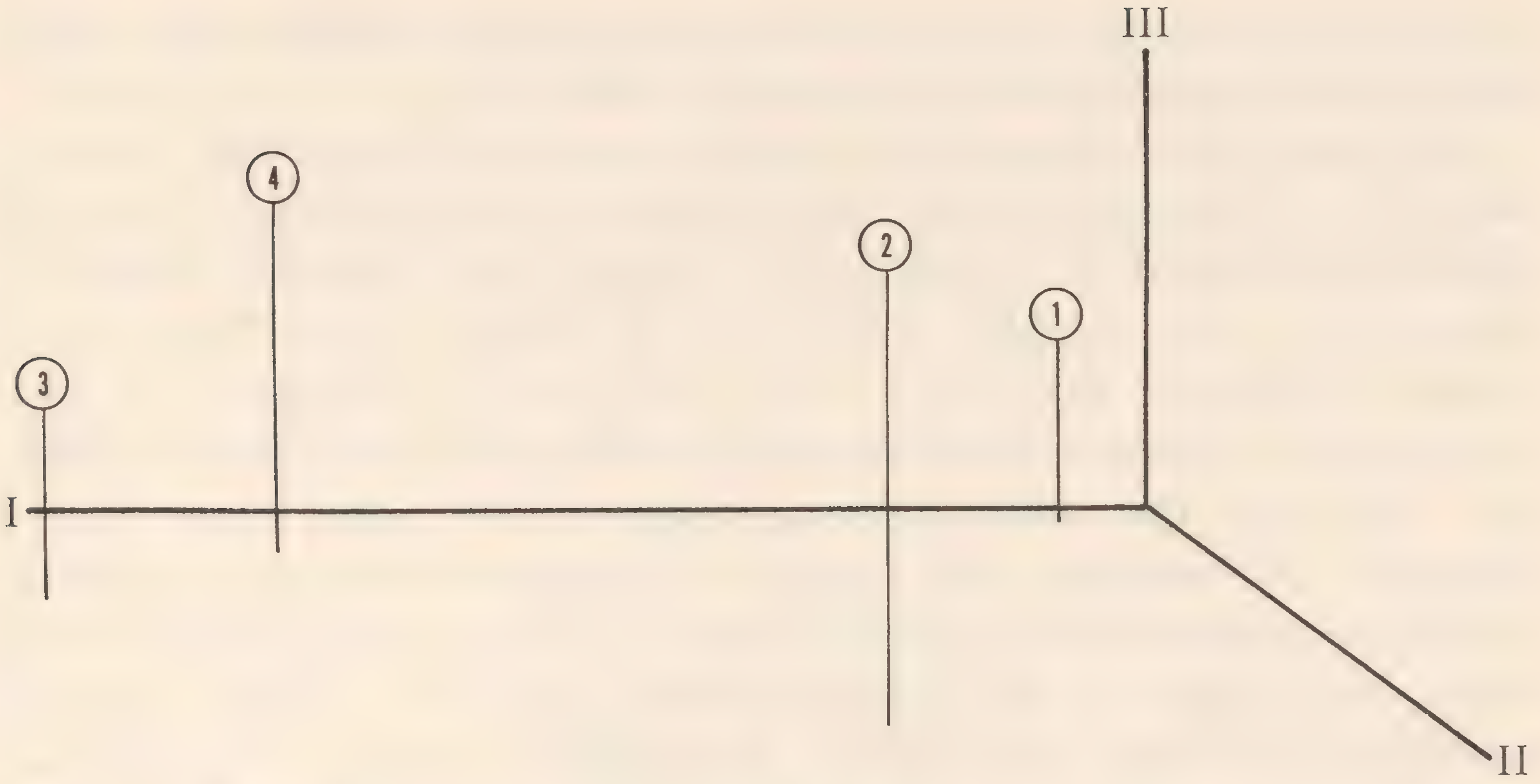

FIG. 4.—Three-dimensional projection of the four study populations of *Microtus mexicanus* onto the first three principal components based on a matrix of correlation among four sperm measurements. Localities are coded as in Fig. 1.

Bacular Morphology

Anderson (1960) described the baculum of *Microtus mexicanus*, and I noted no major deviations from his description. Of the 64 bacula examined, 20 possessed neither medial nor lateral processes; 32 possessed only the medial process; and 12 possessed both. Accordingly, of the five bacular measurements taken, only three (bacular length, width of base, and width of shaft) were consistently available for all specimens.

Mean values, followed by range in parentheses and sample sizes for selected bacular measurements were (measurements are in microns and localities are given in the order Beartrap, 4th of July, South Fork, and Guadalupe): *bacular length*, 2.81(2.37-3.76) 18; 2.98(2.07-3.53) 13; 2.69(2.05-3.21) 15; 2.90(2.52-3.23) 16; *width of base*, 1.35(0.98-1.85) 18; 1.36(0.55-1.87) 13; 1.25(0.71-1.77) 15; 1.39(0.97-1.71) 16; *width of shaft*, 0.27(0.16-0.37) 18; 0.28(0.17-0.38) 13; 0.27(0.17-0.38) 15; 0.30(0.22-0.40) 16. Univariate analysis of these three measurements revealed no significant differences among specimens from the four localities. The large amount of individual variation (CV's, 7.3-30.2) evident in bacular morphology, even among individuals of similar size (and presumably similar age), makes statistical treatment of bacular measurements difficult. Bacula enlarge and change somewhat in shape throughout life. Although dividing the bacula into age classes would reduce variation due to age, estimating the age of individual microtines is difficult, and the small number of bacula available rendered an attempt to age specimens unfeasable at this time.

Although there have been several surveys of microtine bacula, few have treated bacular measurements statistically. Dearden (1958) performed an analysis of variance and reported standard errors for some bacular characters in several microtines. His results indicated that there were subspecific differences in the length of the bacular shaft in several subspecies of *Lagurus curtatus*, although the standard errors were nearly twice those that I found in the bacular shaft length of *Microtus mexicanus*. Coefficients of variation for bacular characters in the Mexican vole were large, compared to the corresponding statistic for any cranial measurement. This high degree of variation within a population, coupled with small sample sizes, makes interpopulational comparisons difficult. As a result, bacular morphology offered no information concerning relationships among the populations examined in this study.

Morphometric Analysis

Fourteen cranial and four external measurements were analyzed using the SAS univariate program. Descriptive statistics and results of the SS-STP tests for these measurements are given in Table 2. Coefficients of variation obtained for the cranial characters (3.26-8.95) agree with those values reported by Long (1968) for rodents.

A two-way analysis of variance was conducted to detect possible sexual dimorphism and to determine if differences existed among localities for cranial and external characters. Differences were found between sexes for depth of skull, total length, and length of hind foot below the probability level of 0.05; for interorbital breadth, 0.01. Total length of females was consistently greater than that of males, and the interorbital breadth was always larger in males than it was in females. Within the Beartrap population, females had deeper skulls and longer hind feet than did males; in the other three populations, males were larger than females in these two characters.

For diastema length, condylozygomatic length, lambdoidal breadth, and length of hind foot, there was no significant difference among localities. Nonoverlapping subsets were found in only two characters: the incisive foramen in specimens from the Guadalupe Mountains was significantly longer than in those from the other three populations; interorbital breadth was larger

TABLE 2.—*Descriptive statistics derived from two-way analysis of variance for external and cranial measurements of* Microtus mexicanus. *Groups of means found to be significantly different at* P>*0.05 were tested with the sums of squares simultaneous testing procedure to find the nonoverlapping subsets. Groups of means that were found to be not significantly different at* P>*0.05 are marked ns. Localities are coded as in Fig. 1.*

Locality	Results SS-STP	Mean	Range	SE	CV
Total length of skull					
2	│	25.5	23.0-27.6	.10	4.29
1	│ │	25.4	23.1-27.6	.13	4.02
4	│ │	25.4	23.0-27.2	.16	4.51
3	│	25.1	22.8-27.4	.09	3.68
Diastema length					
1		7.8	6.7-9.1	.06	5.72
2		7.7	6.7-8.7	.04	5.41
3	ns	7.7	6.7-8.8	.04	5.36
4		7.6	6.9-8.6	.05	5.26
Length of incisive foramen					
4	│	4.7	4.1-5.3	.05	7.27
1	│	4.5	3.5-5.4	.03	6.22
3	│	4.5	3.8-5.3	.03	6.38
2	│	4.4	3.4-5.3	.04	8.59
Palatilar length					
1	│	13.0	11.5-14.3	.07	4.28
2	│ │	13.0	11.7-14.2	.05	4.25
3	│ │	12.8	11.3-14.1	.05	3.92
4	│	12.8	11.5-14.2	.08	4.82
Condylozygomatic length					
1		19.2	17.5-20.7	.03	3.49
2		19.2	17.6-20.8	.07	3.87
3	ns	19.2	17.6-12.1	.06	3.26
4		19.4	17.7-20.8	.10	3.95
Length of nasals					
2	│	7.7	6.1-9.0	.04	5.71
1	│ │	7.6	6.0-8.4	.07	6.97
3	│ │	7.5	5.9-8.6	.04	6.19
4	│	7.3	6.2-8.1	.06	6.24
Rostral breadth					
4	│	4.1	3.7-4.5	.03	4.80
2	│	4.1	3.7-4.5	.02	4.44
1	│ │	4.1	3.7-4.6	.02	4.78
3	│	4.0	3.6-4.8	.02	4.32

Table 2.—*Continued.*

				Interorbital breadth (males)			
2	│			3.4	2.9-3.9	.03	7.26
1	│			3.4	3.0-3.6	.03	4.76
4		│		3.2	2.8-3.6	.04	6.07
3		│		3.2	2.7-3.9	.03	6.66
				Interorbital breadth (females)			
1	│			3.4	2.9-3.8	.04	7.58
2	│			3.3	2.9-3.8	.03	6.87
4		│		3.2	2.7-3.7	.04	6.56
3		│		3.1	2.4-3.6	.03	6.76
				Zygomatic breadth			
4	│			15.0	13.3-16.7	.10	5.00
1	│	│		14.7	13.1-16.0	.08	4.57
3		│		14.7	13.4-16.4	.06	4.04
2		│		14.7	12.8-16.1	.06	4.60
				Prelamboidal breadth			
2	│			10.5	9.5-11.7	.03	3.54
4	│	│		10.4	9.4-11.2	.05	3.53
1		│		10.3	9.4-11.0	.04	3.34
3		│		10.3	9.5-11.8	.03	3.56
				Lambdoidal breadth			
1				11.7	10.6-12.6	.06	4.03
2				11.7	10.5-12.6	.04	3.90
3		ns		11.5	10.1-12.4	.04	3.85
4				11.5	10.2-12.4	.07	4.70
				Height of skull			
2	│			10.0	9.2-11.0	.03	3.29
1	│	│		9.9	9.0-11.2	.05	4.10
4	│	│		9.9	9.2-10.9	.06	4.10
3		│		9.8	9.0-10.6	.03	3.46
				Depth of braincase (males)			
2	│			7.8	7.3-9.2	.04	4.21
3	│	│		7.7	7.0-8.8	.05	4.75
4		│	│	7.6	7.1-8.2	.07	4.03
1			│	7.4	6.3-8.1	.08	5.42
				Depth of braincase (females)			
2	│			7.8	7.1-8.5	.04	3.68
1	│	│		7.7	6.9-8.5	.06	4.87
3		│		7.6	6.9-8.6	.05	4.64
4		│		7.4	6.7-8.3	.07	5.13

TABLE 2.—*Continued.*

Rostral length							
2	│			6.3	4.9-7.3	.05	8.23
1	│	│		6.2	4.9-7.5	.07	8.91
4		│	│	6.0	4.7-7.3	.07	8.95
3			│	5.9	4.7-7.1	.04	7.68
Total length (males)							
1				127.1	111.0-148.0	2.01	8.23
2				131.2	107.0-150.0	1.18	6.87
3	ns			131.2	119.0-148.0	1.05	5.80
4				127.4	114.0-140.0	1.75	6.30
Total length (females)							
1				130.4	95.0-151.0	1.91	8.90
2				134.3	109.0-173.0	1.63	9.17
3	ns			134.1	110.0-158.0	1.38	7.84
4				129.2	111.0-152.0	1.82	8.09
Length of tail							
4	│			30.9	22.0-42.0	.48	11.34
2	│	│		29.5	22.0-58.0	.42	15.13
1		│		28.7	15.0-42.0	.55	15.30
3		│		28.3	18.0-39.0	.37	13.58
Length of hind foot (males)							
1				17.3	15.0-20.0	.21	6.35
2				17.8	15.0-22.0	.19	8.15
3	ns			17.5	16.0-19.0	.14	5.79
4				17.7	15.0-20.0	.37	9.53
Length of hind foot (females)							
1				17.5	15.0-20.0	.19	6.70
2				17.2	12.0-23.0	.22	9.85
3	ns			17.2	16.0-20.0	.12	5.36
4				17.5	15.0-21.0	.29	9.37
Length of ear							
4	│			12.7	10.0-18.0	.25	14.19
2	│	│		12.4	9.0-19.0	.14	12.28
1	│	│		12.1	10.0-19.0	.17	11.55
3		│		12.0	9.0-15.0	.10	8.32

in individuals from Beartrap and 4th of July populations than those from South Fork and Guadalupe localities. The remaining characters showed from two to three overlapping subsets but provided no distinct groupings.

Characters with high coefficients of variation (length of tail and length of ear) and the four characters which displayed sexual dimorphism (depth of skull, total length, length of hind foot, and interorbital breadth) were eliminated from the subsequent multivariate analyses. The remaining 12 cranial measurements were then analyzed using the NT-SYS multivariate analysis program. Correlation and distance matrices were computed and phenograms representing the phenetic relationships of the four OTU's were plotted. In addition, a Pearson product-moment correlation was computed comparing these two morphometric matrices with the corresponding electrophoretic matrices. The correlation coefficients for the two distance matrices and for the two correlation matrices were not significant. The distance phenogram for morphometric characters differed from that produced for sperm measurements presented earlier, with two clusters: Beartrap, 4th of July, and South Fork forming the first, and Guadalupe forming the second.

The first three principal components were extracted and plotted, yielding the relationships illustrated in Fig. 5. Phenetic variation expressed by the first principal component was 54.78 per cent; second, 37.75; third, 7.47. The major contributing characters for each component and their percentage contribution were: first principal component: total length of skull (14.48), palatilar length (13.27), condylozygomatic length (11.34), zygomatic breadth (12.95), and lambdoidal breadth (12.40); second component: total length of skull (27.42) and condylozygomatic length (20.62); third component: total length of skull (15.55) and prelambdoidal breadth (18.74). Thus, characterization of the OTU's by principal components is, to a large degree, dependent on total length of skull. The three-dimensional plot arranged the OTU's into two groups that corresponded to those of the distance phenogram. The Beartrap and 4th of July samples were again grouped much closer to each other than to the South Fork and Guadalupe samples. The latter two populations are separated somewhat along axis II.

Thus, morphometric analyses yielded no conclusive evidence concerning relationships of the four populations studied. The four populations examined generally fell into two groups, corresponding to the same two groups produced by analysis of sperm morphology. There is some evidence from the phenogram based on morphometric characters and the results of the SS-STP test that the Guadalupe population is more distinct than the other three populations. The Guadalupe population has a significantly longer incisive foramen. However, for interorbital breadth, the Beartrap and 4th of July populations have relatively greater interorbital breadth than the South Fork and Guadalupe samples.

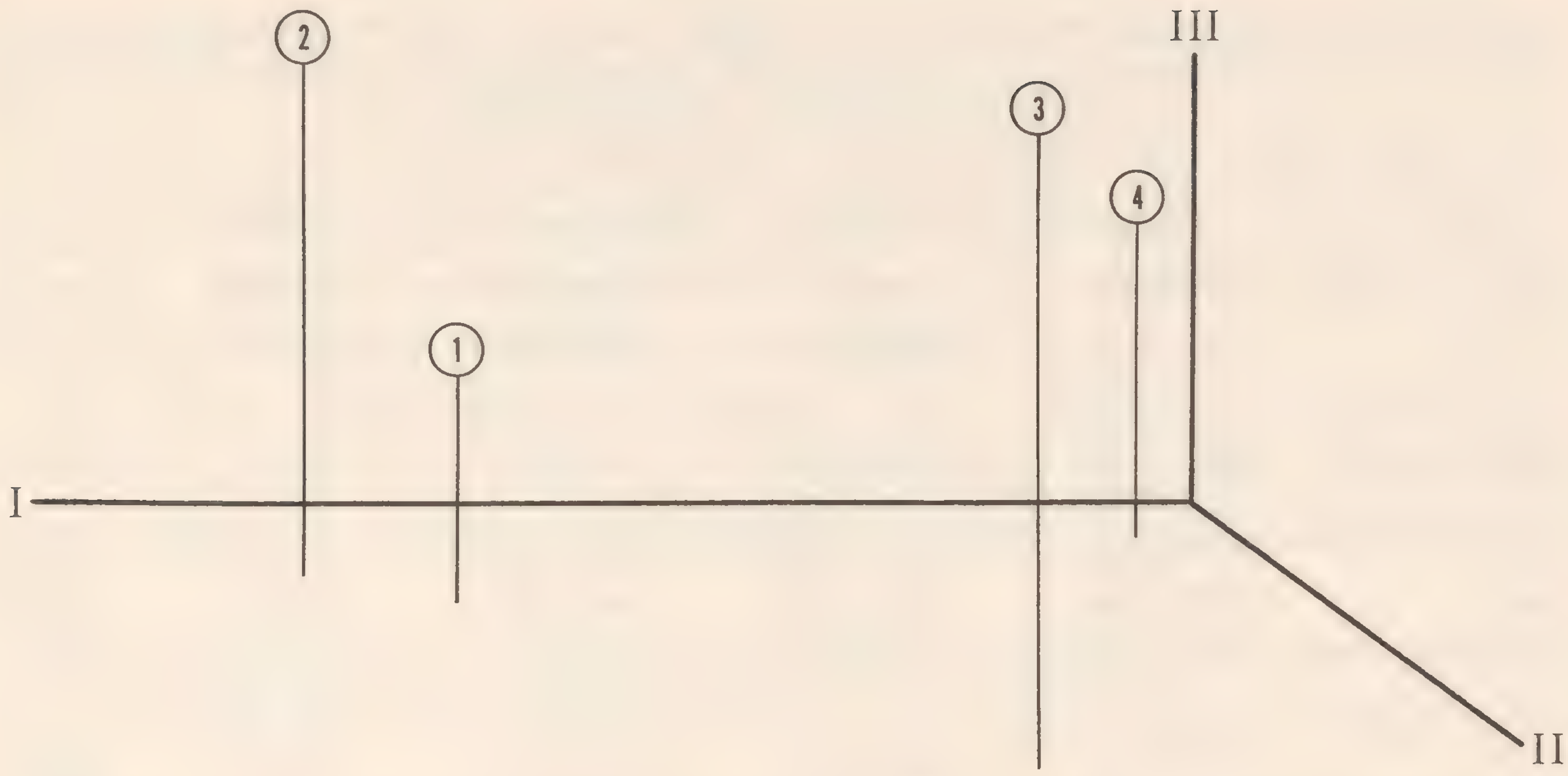

Fig. 5.—Three-dimensional projection of the four study populations of *Microtus mexicanus* onto the first three principal components based on a matrix of correlation among 12 cranial measurements. Localities are coded as in Fig. 1.

Principal component analyses separated the four populations into the same two groups identified in the sperm analysis and in the morphometric phenogram.

Microtine subspecies generally have been delimited by size differences as well as qualitiative characteristics, such as pelage color. *Microtus mexicanus guadalupensis* was distinguished by Bailey (1902) from *M. m. mogollonensis* primarily on the basis of cranial characters. Bailey (1902) reported measurements for the male holotype of *M. m. guadalupensis*, six of which may be compared with those taken in this study: total length, 152; length of tail, 34; length of hind foot, 20; basal length of skull, 24.5; length of nasals, 7.5; and zygomatic breadth, 16.0. A comparison of these measurements with those in Table 2 reveals that the total length of the holotype exceeds that of any Guadalupe male examined, and equals that of the largest Guadalupe female examined. The tail of the holotype was longer than the average length of tail found in this study, and the length of hind foot equals the largest value reported herein. The three skull measurements of the holotype all are near the average for those measurements in the Guadalupe specimens examined.

Electrophoretic Analysis

Nineteen protein systems were investigated, but only 16 were scored with confidence. These systems contained 24 scorable loci, which are listed in Table 3 along with the frequencies of each in the population. In the total sample, 14 loci (58 per cent) were polymorphic, and five (LDH-2, ADH, G-6-P, MDH-1, and EST-7)

TABLE 3.—*Alleles and frequencies (in parentheses) at 24 loci in* Microtus mexicanus *and the mean proportion of individuals heterozygous at each locus ($\bar{h}$); $\bar{h}$ is averaged over all four populations (N=80).*

Locus	Beartrap	4th of July	South Fork	Guadalupe	$\bar{h}$
LDH-1	100(1.00)	100(1.00)	100(1.00)	100(1.00)	0.00
LDH-2	100(.975) 72(.025)	100(1.00)	100(1.00)	100(1.00)	0.01
MDH-1	100(.975) 70(.025)	100(1.00)	100(1.00)	100(1.00)	0.01
MDH-2	−100(1.00)	−100(1.00)	−100(1.00)	−100(1.00)	0.00
ME	100(1.00)	100(1.00)	100(1.00)	100(1.00)	0.00
IDH	100(1.00)	100(1.00)	100(.925) 85(.075)	100(.650) 85(.350)	0.19
SDH	100(1.00)	100(1.00)	100(.950) 116(.050)	100(1.00)	0.03
ADH	−100(1.00))	−100(.825) −86(.175)	−100(.950) −86(.050)	−100(1.00)	0.11
LAP	100(1.00)	100(1.00)	100(1.00)	100(1.00)	0.00
PGI	100(.750) 54(.250)	100(.800) 33(.200)	100(.800) 54(.200)	100(.250) 54(.750)	0.40
PGM	100(.825) 160(.175)	100(1.00)	100(1.00)	100(1.00)	0.06
AB	100(1.00)	100(1.00)	100(1.00)	100(1.00)	0.00
IPO	100(1.00)	100(1.00)	100(1.00)	100(1.00)	0.00
GOT-1	100(1.00)	100(1.00)	100(1.00)	100(1.00)	0.00
GOT-2	−100(1.00)	−100(.900) −41(.100)	−100(.700) −41(.300)	−100(1.00)	0.15
G-6-P	100(1.00)	100(1.00)	100(1.00)	100(.975) 88(.025)	0.01
GDH-1	100(1.00)	100(1.00)	100(1.00)	100(1.00)	0.00
GDH-2	100(1.00)	100(1.00)	100(1.00)	100(1.00)	0.00
GDH-3	100(1.00)	100(1.00)	100(1.00)	100(1.00)	0.00
αGPDH-1	100(1.00)	100(.950) 115(.050)	100(1.00)	100(1.00)	0.03
αGPDH-2	100(.925) 129(.050) 90(.025)	100(.975) 129(.025)	100(.950) 129(.050)	100(.975) 129(.025)	0.09
αGPDH-3	100(.925) 142(.075)	100(1.00)	100(.950) 142(.050)	100(1.00)	0.04
EST-1	100(.475) 93(.525)	100(.800) 93(.200)	100(.850) 93(.150)	100(.925) 93(.075)	0.43
EST-7	100(.975) 65(.025)	100(.975) 65(.025)	100(1.00)	100(1.00)	0.03

were present in a frequency of only five per cent. Acid phosphatase (ACP), alkaline phosphatase (AKP), and xanthine dehydrogenase (XDH) were incompletely scored, but did exhibit some polymorphism. The major features of the allozyme variations observed in *Microtus mexicanus* are listed below.

Malate dehydrogenase (MDH).—Two MDH loci were observed; the cathodally migrating MDH-2 was monomorphic for all populations. MDH-1 exhibited two alleles; the MDH-1^{70} allele was present in a single specimen from Beartrap.

Isocitrate dehydrogenase (IDH).—This system was represented by two alleles. The IDH^{85} allele was found in three individuals from South Fork and in 13 individuals from the Guadalupe sample.

Sorbitol dehydrogenase (SDH).—Two SDH alleles were identified; the SDH^{116} allele was found in two individuals from South Fork.

Alcohol dehydrogenase (ADH).—Two ADH alleles were observed in this cathodally migrating system. The ADH^{-86} allele was present in seven individuals from 4th of July and in two individuals from South Fork.

Phosphoglucose isomerase (PGI).—Three alleles were represented in this system. The PGI^{100} allele occurred in all samples. PGI^{54} was identified in eight individuals from Beartrap, eight from South Fork, and in all individuals from Guadalupe. PGI^{33} was present in eight specimens from the 4th of July Campground.

Phosphoglucomutase (PGM).—This locus was represented by two alleles. All populations exhibited the PGM^{100} allele; PGM^{160} was identified in six individuals from Beartrap.

Glutamate oxalate transaminase (GOT).—Two loci were observed; GOT-1 was monomorphic for all populations, and the polymorphic GOT-2 allele migrated cathodally. Four individuals from the 4th of July sample and 10 from South Fork exhibited the GOT-2^{-41} allele.

Glucose-6-phosphate dehydrogenase (G-6-P).—Two alleles were observed; the G-6-P^{100} allele was represented in all populations; the G-6-P^{88} allele was found in one individual from the Guadalupe sample.

αGlycerophosphate dehydrogenase (αGPDH).—Three loci were identified and all exhibited polymorphism. The αGPDH-1^{115} allele was found in two individuals from 4th of July. αGPDH-2 was represented by three alleles; all populations exhibited the α GPDH-2^{100} and αGPDH-2^{129} alleles, and the αGPDH-2^{90} allele was present in only one specimen from Beartrap. αGPDH-3^{142} was detected in two specimens from Beartrap and in two from South Fork.

Table 4.—*Proportion of individuals heterozygous per locus per population (h). P is the proportion of 24 loci polymorphic in each population (loci with commonest allele at a frequency of >0.95 were considered monomorphic); $\bar{H}$, mean proportion of loci heterozygous per individual, N = 20.*

Locus	Populations sampled			
	Beartrap	4th of July	South Fork	Guadalupe
LDH-2	.05			
MDH-1	.05			
IDH			.15	.60
SDH			.10	
ADH		.35	.10	
PGI	.30	.40	.40	.50
PGM	.25			
GOT-2		.20	.40	
G-6-P				.05
αGPDH-1		.10		
αGPDH-2	.15	.05	.10	.05
αGPDH-3	.05		.10	
EST-1	.45	.40	.20	.15
EST-7	.05	.05		
P	.166	.208	.353	.125
$\bar{H}$	.054	.065	.065	.056

Esterases (EST).—A total of seven esterase systems were identified, but only two could be scored with confidence. EST-1 contained two alleles found in all four populations. EST-7 also was composed of two alleles; EST-7^{65} was found in one specimen from Beartrap and in one from 4th of July Campground. Of the five remaining esterases identified, EST-2 and EST-3 exhibited polymorphism in all populations. EST-4 and EST-5 were polymorphic in all populations except that from the Guadalupe Mountains, and EST-6 was monomorphic in all populations.

Monomorphic proteins.—The following proteins were scored as monomorphic in all populations sampled: lactate dehydrogenase (LDH); malate dehydrogenase-2 (MDH-2); malate enzyme (ME); leucine aminopeptidase (LAP); albumin (AB); indolphenol oxidase (IPO); glutamate oxalate transaminase-1 (GOT-1); and glutamate dehydrogenase-1, −2, −3 (GDH-1, GDH-2, GDH-3).

Genic variability.—Table 4 gives the proportion of polymorphic loci in each population, the proportion of heterozygous loci per individual, and the proportion of heterozygous individuals per locus per population. Genic heterozygosity (H) is based on the analysis of 24 loci (14 polymoprhic, 10 monomorphic).

TABLE 5.—*Coefficients of genic similarity (Rogers' S), genic identity (Nei's I), and genetic distance, (Nei's D), respectively, for four populations of* Microtus mexicanus.

	Beartrap	4th of July	South Fork	Guadalupe
Beartrap	1.0000	0.9535	0.9401	0.9279
	0.0000	0.9883	0.9847	0.9526
	0.0000	0.0117	0.0155	0.0486
4th of July		1.0000	0.9572	0.9142
		0.0000	0.9933	0.9543
		0.0000	0.0067	0.0468
South Fork			1.0000	0.9119
			0.0000	0.9566
			0.0000	0.0444
Guadalupe				1.0000
				0.0000
				0.0000

The loci that contributed most to the heterozygosity values varied among populations. Phosphoglucose isomerase (PGI) was a major contributor in all populations, whereas EST-1 was responsible for most of the individual heterozygosity in the Beartrap and 4th of July populations. Other loci contributing significant amounts of heterozygosity were PGM in Beartrap, ADH in 4th of July, GOT-2 in South Fork, and IDH in the Guadalupe sample.

The Beartrap population exhibited four unique alleles (LDH-2^{72}, MDH-1^{70}, PGM^{160}, and αGPDH-2^{90}), whereas the 4th of July population possessed only two unique alleles (PGI^{33} and αGPDH-1^{115}). The remaining two populations had one unique allele each; South Fork (SDH^{116}) and Guadalupe (G-6-P^{88}).

Genic similarity.—Coefficients of genic similarity between populations were calculated, using Rodgers' similarity, S (Rodgers, 1972) and Nei's identity, *I* (Nei, 1972). Values for *I* are generally slightly higher than those for *S*, but both measures give comparable results. Both are reported in Table 5.

Electrophoretic studies generally show high levels of polymorphism in natural populations, with reduced levels of heterozygosity in small, isolated populations. Selander *et al.* (1971) demonstrated low levels of genic variability ($\overline{H} = 0.018$) in insular populations of *Peromyscus polionotus* compared to the larger mainland populations ($\overline{H} = 0.054$-0.088). Similar results were obtained for several species of *Peromyscus* (Avise *et al.*, 1974*b*), in which insular subspecies had an average of less than one per cent heterozygous loci. Reduced levels of heterozygosity in small, isolated populations are thought to be due to genetic drift.

The level of genetic variability is relatively uniform for the four populations of Mexican voles studied, ranging from 0.054 to 0.065 (mean, 0.060). These values are consistent with heterozygosity values for other mainland vertebrate populations ($\overline{H}$ = 0.01-0.09) as reported by Selander and Johnson (1973). The proportion of the 24 loci examined that were polymorphic (P) ranged from 0.125 to 0.353 (mean, 0.213). This figure also agrees with the value of 0.202 that Selander (1976) listed as an average value for rodents.

Rodgers' coefficient of genic similarity (S) between the Guadalupe sample and the other three populations studied is less than 0.93, whereas those between the other three all are more than 0.94. This relationship is more pronounced in Nei's identity coefficient, where the values separating the Guadalupe sample and the remaining populations are less than 0.96; those between the other three are greater than 0.98. Coefficients of similarity generally range from 0.90 to 1.00 for conspecific populations of rodents, although in strongly divergent populations of *Peromyscus polionotus* on Florida's barrier islands, the average similarity value drops to 0.84 (Selander and Johnson, 1973).

Other biochemical studies comparing subspecies have yielded Rodgers' similarity values of 0.769 in *Mus musculus* (Selander *et al.*, 1969), 0.89 to 0.95 in *Peromyscus boylii*, and 0.75 to 0.79 in *P. polionotus* (Avise *et al.*, 1974*a*), and 0.86 in *P. eremicus* (Avise et al., 1974*b*). The low values for *Mus* in reality could be due to the fact that the two subspecies studied are incipient species, whereas those reported for *P. polionotus* result from comparison of a subspecies occurring on Florida's barrier islands to a mainland population. The values obtained in this study ranged from 0.9119 to 0.9572, and, because these are well within the range of values reported for other rodent subspecies, would seem to indicate that the populations examined are no more differentiated than would be expected on the basis of their current taxonomic rank. Unfortunately, no data from other microtines are available for comparison.

Electrophoretic analysis revealed a close association among all four populations studied, but also indicated that there could be some slight differences between the Guadalupe population and the remaining three.

Inconsistencies in the morphometric and electrophoretic analyses result from two different approaches to the same problem and are to be expected. Electrophoretic analysis frequently fails to distinguish between or among subspecies that were described initially on the basis of classical systematic criteria. Whether many subspecies are arbitrary units that do not reflect major gene differences or whether the resolution resulting from electrophoretic techniques is insufficient to detect the differences is not known at present, but both elements probably are involved (Avise, 1975). Contrasts between genic similarity and organismic similarity are not unknown, and it might be a general rule that organismic evolution and stuctural gene evolution proceed at virtually independent rates, as suggested by Wilson (1976). Therefore, in this study, electrophoretic evidence was accorded less consideration than were other data in determining systematic placement of the four populations.

Chronology

Findley (1969) explained many of the present mammalian distributional patterns in the southwestern United States on the basis of a series of boreal expansions and contractions in the late Pleistocene, the contractions leaving isolated boreal habitats and populations of certain mammals on scattered mountain ranges. The Mexican vole was probably widespread over the Mexican and Colorado plateaus during the cooler, more mesic pluvial periods of the late Pleistocene. The aridity of interpluvial periods caused fragmentation of the distribution of that vole, and with increasing aridity, those fragments became restricted to relatively mesic mountaintops (see also Smartt, 1977).

The chronology of late Pleistocene events in the southwestern United States was estimated by Wendorf (1975), based on pollen profiles from the Llano Estacado of West Texas. Evidence of a continuous boreal forest on the Llano as low as 1000 meters during the Early Tahoka Pluvial (17,000 BP) corresponds to a depression of vegetative zones of from 1300 to 1500 meters below their current levels. Because intermontane altitudes in the area under study range from about 1250 to 2050 meters, the presence of more or less continuous boreal forest there in the Early Tahoka seems probable.

The Late Tahoka Pluvial, dated approximately 11,500 BP, evidently was the most recent period of extensive pine-spruce forest in this area (Wendorf, 1975). This rather open forest covered much of the Southwest, as evidenced by the fact that the Llano Estacado was at least 50 per cent covered by spruce-pine forest (Wendorf, 1961). During this pluvial period, then, the Mexican vole was probably still widely distributed over Arizona, New Mexico, and western Texas. *M. mexicanus* was present on the Llano Estacado at this time in extreme eastern New Mexico, at an elevation of 1350 meters in what is now Roosevelt County (Slaughter, 1975).

Fragmentation in the distribution of *Microtus mexicanus* probably began with the Scharbauer Interval (10,500 BP), which marked the end of the Late Tahoka Pluvial. This was a time of increasing aridity and was marked by a decline of the pine-spruce forest in the Southwest, although subsequent periods of resurgence of cooler and more moist conditions could have allowed temporary expansion of boreal habitats. The boreal extensions, both in time and geographic scope, since the late Tahokan are not presently known, but in all likelihood they were not of sufficient magnitude to connect previously isolated montane habitats. The climate of the Southwest has been one of increasing aridity since the Lubbock Subpluvial (9500 BP) and has undoubtedly resulted in the progressive geographic isolation of boreal elements on mountain tops.

The subspecies of *Microtus mexicanus* in this study almost certainly result from 9000 to 10,000 years of isolation (Slaughter placed the isolation of *M. mexicanus* at post-10,000 BP). The degree of differentiation observed between the two nominal taxa provides, therefore, some idea of the gross rate of evolution in this species, and, in a general way, underscores the relationship between geographic isolation and evolution in a small mammal.

Relative divergence times (T) for paired combinations of all populations were calculated following Nei's (1971*a*) technique using the expected number of amino acid differences (D) per protein that can be detected by electrophoresis. Nei (1971*b*) renamed the function D, calling it "genetic distance," and later presented a detailed description (Nei, 1972). Genetic distance is defined as $D = -\log_e I$, where I is Nei's identity value. The values of Nei's genetic distance are given in Table 5. Relative divergence times were then estimated using the formula $T = D_1/D_2$, where D_1 and D_2 are the genetic distance values for the population pairs in question, and are presented in Table 6. Using this table, it is possible to postulate the order of divergence of the four populations by listing the population pairs from one column in order of increasing divergence times. This suggests the following sequence of events. Isolation of the Guadalupe population (4) occurred first. It initially was separated from the Beartrap population (1), followed quickly by separation from the 4th of July (2) and South Fork (3) popula-

TABLE 6.—*Matrix of relative divergence times (T). Parentheses indicate exceptions from the general order discussed in the text. Pairs of populations compared on both the ordinate and abcissa are the same as coded in Fig. 1.*

D_1	1,2	1,3	1,4	2,3	2,4	3,4
D_2						
1,2	1.00	1.32	4.15	0.57	4.00	3.79
1,3	0.75	1.00	3.14	0.43	3.02	2.86
1,4	0.24	0.32	1.00	0.137	(0.80)	(0.91)
2,3	1.75	2.31	7.25	1.00	(6.08)	(6.63)
2,4	0.25	0.33	1.04	0.143	1.00	0.95
3,4	0.26	0.35	1.09	0.15	1.05	1.00

tions. The next population to be isolated was that at Beartrap. It was first separated from South Fork, then from 4th of July. The last separation isolated the 4th of July and the South Fork populations. It can be seen from the geographic relationships of the four study areas (Fig. 1), that the isolation of Guadalupe from South Fork probably occurred at about the same time as separation of the Guadalupe-4th of July and of the Guadalupe-Beartrap populations.

Inasmuch as the calculation of relative time of divergence is intimately related to Nei's identity value (I), it is not surprising that these values correlate perfectly with the hypothetical sequence (derived from observed divergence of characters) of isolation of the four populations studied. The highest identity values are found between those populations theoretically in contact for the longest period of time. Rodgers' similarity values (S) indicate the same situation, except that they suggest that the Guadalupe population was in contact with the Beartrap population for a slightly longer period than it was with either the South Fork or the 4th of July populations.

Although the calculation of relative divergence times can offer only gross estimates of temporal isolation, the sequence of events indicated by these data agrees with what would be expected from examination of the geologic evidence. Other recent studies on mammals have shown that Nei's evolutionary divergence time does correlate well with both fossil and morphological evidence (Nevo *et al.*, 1974; Zimmerman *et al.*, 1975; Kilpatrick and Zimmerman, 1976). As the Pleistocene glaciers retreated northward and the climate of the Southwest became warmer and drier, boreal taxa such as the Mexican vole were forced into isolation on montane refugia. Such restrictions evidently first took place on the southernmost Guadalupe Mountains, was followed by isolation of the Beartrap population west of the Rio Grande on the San Mateo Mountains, and ended with isolation of the 4th of July and South Fork populations on the Manzano and Sacramento mountains, respectively. It is significant to note that the population thought to have been isolated for the longest period of time is the one showing the greatest degree of genic and morphological differentiation.

Results of this study indicate that *Microtus mexicanus* is an evolutionarily conservative microtine. Only slight change evidently has taken place in isolated populations of the species over a time span in which several European microtines have developed well-marked karyotypic and morphologic differences. No other North American microtine has been the subject of a detailed systematic investigation, however, and the Mexican vole could prove to be an exceptionally conservative species.

Taxonomic Conclusions

Subspecific differentiation of *Microtus mexicanus* in the region of study undoubtedly has occurred since the isolation of populations on mountain ranges in the late Pleistocene. The current subspecific boundries were established by Bailey (1932), with the Rio Grande designated as the line of demarcation between *M. m. mogollonensis* (occurring in the mountains to the west of the river) and *M. m. guadalupensis* (inhabiting montane areas to the east). This arrangement seems logical in a geographic sense, and places the Beartrap sample (San Mateo Mountains) in the subspecies *mogollonensis* and the remaining three samples (4th of July, Manzano Mountains; South Fork, Sacramento Mountains; and Guadalupe, Guadalupe Mountains) in the subspecies *guadalupensis.*

Results of the sperm and morphometric analyses demonstrate, however, that the 4th of July sample bears a closer relationship to the Beartrap sample than it does to either of the other two populations. Therefore, the 4th of July population is here transferred to the subspecies *M. m. mogollonensis.* The South Fork and Guadalupe populations remain referrable to *M. m. guadalupensis.*

There exists, however, a certain degree of divergence between the Guadalupe and South Fork samples, as evidenced by both cranial characters and values of electrophoretic similarity. Considering the isolated nature of these two populations and the degree of divergence exhibited, I conclude that they constitute an example of incipient subspeciation. The Guadalupe Mountains are lower in altitude and considerably drier than are the other three mountain masses. This results in extremely restricted areas of habitat for Mexican voles and severely limits the population size. The Guadalupe sample thus represents a population with several of the attributes typically thought to contribute to evolutionary divergence. Geographic isolation, small population size, occupancy of a heterogenous habitat dividing this population into several smaller demes, and a harsh or stringent environment relative to other conspecific populations, might be reflected in the degree of divergence found in the Guadalupe population of *Microtus mexicanus.*

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A NEW SUBSPECIES OF GLOSSOPHAGA COMMISSARISI (CHIROPTERA: PHYLLOSTOMIDAE) FROM WESTERN MEXICO

WM. DAVID WEBSTER AND J. KNOX JONES, JR.

Glossophaga commissarisi originally was described by Gardner (1962) on the basis of specimens from the Mexican states of Chiapas, Colima, and Nayarit. Subsequent work has shown that the species occurs as far north in western México as central Sinaloa (Jones *et al.*, 1972), and southeastward in Middle America to Panamá (Handley, 1966). No records currently are available from South America, but this bat surely will be found there in at least western Colombia as well.

That specimens of *G. commissarisi* from the northern part of the range of the species in western México (Colima, Durango, Jalisco, Nayarit, and Sinaloa) average larger and somewhat paler in color than bats to the south has been known for some time. Most earlier workers evidently assumed, as we did, that *commissarisi* eventually would be found to be continuously distributed in western México (see Jones and Carter, 1976, and Hall, 1981, for example) and that the northern population probably represented the terminus of clinal variation in size and color. However, extensive field operations in the 20 years that have elapsed since the original description, coupled with our examination of thousands of bats of the genus *Glossophaga* in all major North American collections, now indicate to us that in all likelihood *G. commissarisi* is absent from much of southwestern México (Guerrero, Michoacán, and western Oaxaca) and that a considerable hiatus thus exists between the population to the north and the main

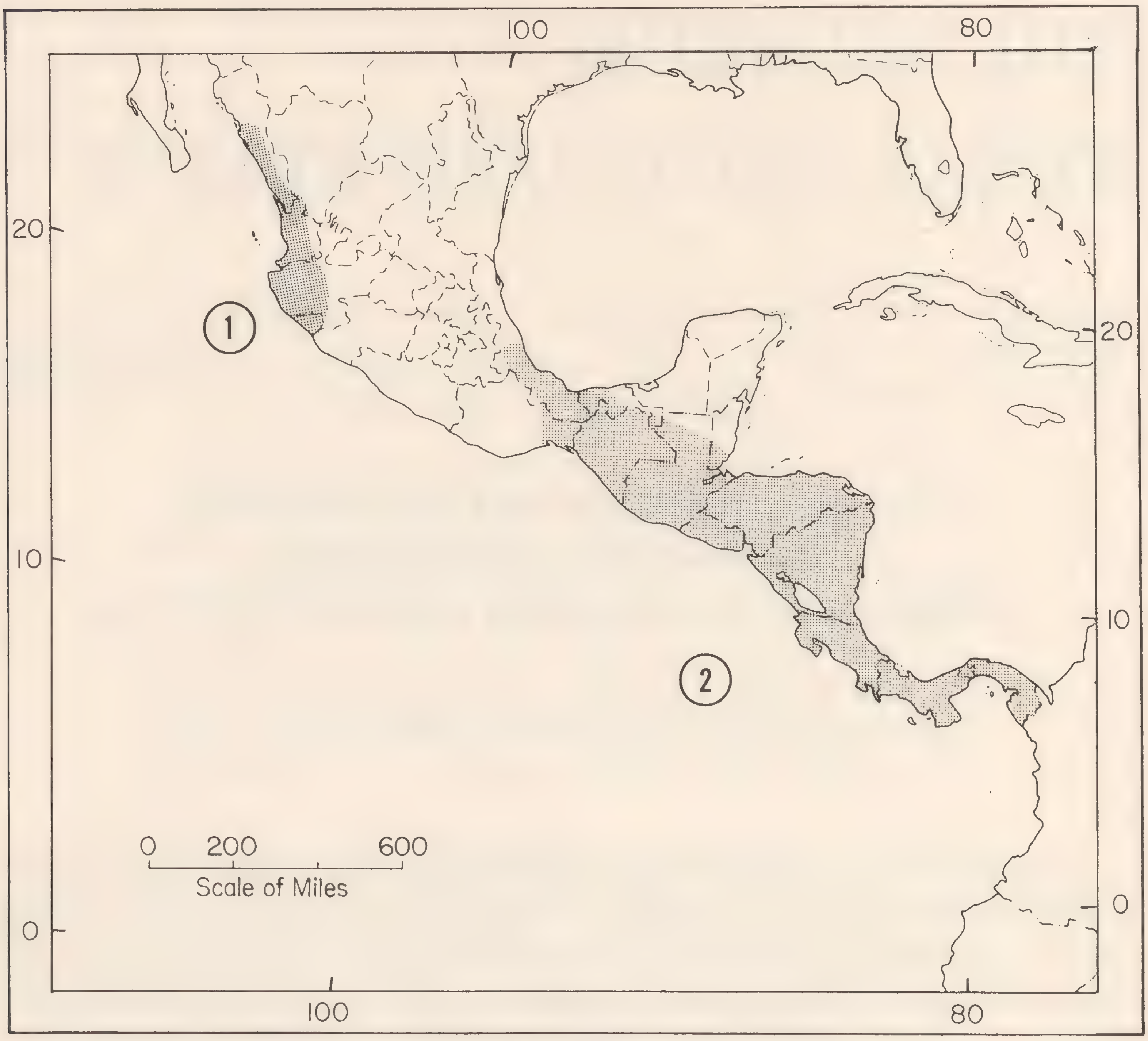

FIG. 1.—Geographic distribution of *Glossophaga commissarisi hespera* (1) and *G. c. commissarisi* (2) in North America.

range of the species to the south (Fig. 1). Inasmuch as Gardner selected a place in Chiapas (10 km. SE Tonalá) as the type locality of *commissarisi*, the northwestern population represents an undescribed subspecies, for which we propose the name:

Glossophaga commissarisi hespera, new subspecies

Holotype.—Adult female, skin and skull, no. 36223, The Museum, Texas Tech University (formerly no. 4956, University of Arizona); from Tepehuajes Mine, *ca.* 20 km. N Soyatlán del Oro, Jalisco; obtained on 16 January 1964 by A. L. Gardner, original no. 6864.

Selected external and cranial measurements (in millimeters) of the holotype are: total length, 75; length of tail, 9; length of hind foot, 11; length of ear from notch, 13; length of forearm (dry), 35.6; greatest length of skull, 21.2; condylobasal length, 19.3; zygomatic breadth, 9.5; mastoid breadth, 9.2; interorbital breadth, 4.2; length of maxillary toothrow, 7.3; length of mandibular toothrow (c-m3), 7.7; weight, 12 grams.

Distribution.—Lowlands and riparian forests of western México from central Sinaloa and southwestern Durango southward to western Jalisco and Colima (Fig. 1); known altitudinal distribution from near sea level to 6000 feet.

Diagnosis.—A large subspecies of *Glossophaga commissarisi*, both externally and cranially (Table 1). The braincase is more domed and the angle between the rostrum and cranium is more abrupt in *G. c. hespera* than in the nominate subspecies. In addition, the posterior presphenoid extension is small, poorly developed, and continuous with the basisphenoid septum in *G. c. hespera*, but is well developed and noticeably raised (in ventral view) from the basisphenoid septum in *G. c. commissarisi*. Although some local variation in color is apparent, *G. c. hespera* averages somewhat paler than *G. c. commissarisi*, resembling the sympatric *Glossophaga soricina handleyi*.

Remarks.—Individuals of *G. c. hespera* have been collected in caves. These bats also have been taken in mist nets over water in various habitats including savanna, arid thorn forest, and subtropical and tropical evergreen forest, particularly along river valleys that penetrate into lower elevations of the Sierra Madre Occidentál. They have been captured frequently at the same locality as has *Glossophaga soricina handleyi*, and the two may be difficult to distinguish in the field. Means by which these and other North American species of *Glossophaga* can be identified were given by Webster and Jones (1980).

Pregnant females are known from January, February, April, July, and September; lactating females have been collected in May. Based on these scanty reproductive data, *G. c. hespera* appears to be polyestrous, with a bimodal cycle (Wilson, 1979).

Specimens examined (42).—COLIMA: Miscuate, 2 (LACM); 11 mi. W Comala, Miscuate, 4 (LACM); Pueblo Juárez, 1 (UA); 5 km. SE Pueblo Juárez, 1 (UA); 35 km. NW Pueblo Juárez, Rancho Tavernillas, 2 (UA); 1 km. S Pueblo Nuevo, 1 (UA); 2.5 km. NW Pueblo Nuevo, 1 (UA). DURANGO: 2 mi. N Pueblo Nuevo, 6000 ft., 1 (MSU); 6 mi. S Pueblo Nuevo, 3000 ft., 1 (MSU). JALISCO: 14 mi. WSW Ameca, 5000 ft., 1 (KU); 8 km. ESE Chamela, 30 m., 1 (MSU); 6 mi. E Limón, 2700 ft., 1 (KU); 2 mi. N. Milpillas, 3000 ft., 1 (KU); 20 km. WNW Purificatión, 1400 ft., 1 (KU); *ca.* 20 km. N Soyatlán del Oro, Tepehuajes Mine, 2 (1 UA, 1 TTU); 10 mi. SE Talpa de Allende, 5300 ft., 1 (KU); 7.5 mi. SE Tecomates, 1500 ft., 1 (KU). NAYARIT: 4 km. S Aticama, 2 (USNM); Chacala, 2 (USNM); Jalcocotán, 1 (USNM); 1 mi. S Lo de Marcos, 2 (USNM); Paso de Soquipa (Zoquipa), 1 (USNM); Río Chilte, 1.2 mi. S El Casco, 480 ft., 1 (USNM); 5 mi. NE San Blas, 1 (KU); 8 mi. E San Blas, 3 (1 LACM, 2 UA); 4 mi. S, 5 mi. E San Blas, 1 (MSB); 5

TABLE 1.—*Selected comparative measurements of* G. c. hespera *and two samples of* G. c. commissarisi. *Mean followed by standard deviation, extremes in parentheses, and sample size.*

		G. c. hespera	*G. c. commissarisi*	
Variate	Sex	(western México)	(vicinity type locality)	(Costa Rica-Panamá)
Length of forearm	♂	34.38±0.90 (32.7-35.6) 12	33.48±1.14 (31.1-35.1) 19	32.78±0.89 (31.3-35.3) 47
	♀	35.00±0.92 (33.2-36.6) 28	33.94±1.18 (32.0-36.6) 21	33.64±0.84 (32.0-35.3) 43
Length of third metacarpal	♂	34.31±1.00 (32.6-35.7) 12	33.49±1.20 (31.7-35.4) 19	32.59±1.02 (30.8-35.6) 47
	♀	34.70±1.03 (33.0-37.3) 28	33.55±1.07 (31.6-36.0) 21	33.41±0.96 (30.8-35.6) 43
Greatest length of skull	♂	20.60±0.27 (20.3-21.1) 12	19.99±0.43 (19.3-21.0) 19	20.11±0.37 (19.1-21.0) 45
	♀	20.67±0.29 (20.2-21.3) 29	20.00±0.26 (19.5-20.5) 21	20.23±0.33 (19.7-21.1) 43
Condylobasal length	♂	18.73±0.18 (18.5-19.1) 12	18.27±0.45 (17.2-19.1) 19	18.44±0.38 (17.5-19.2) 45
	♀	18.84±0.29 (18.3-19.3) 29	18.37±0.29 (17.8-19.0) 21	18.58±0.34 (17.9-19.4) 43
Zygomatic breadth	♂	9.64±0.15 (9.4- 9.9) 12	9.46±0.27 (9.0-10.1) 18	9.30±0.31 (8.6- 9.8) 47
	♀	9.45±0.19 (8.9- 9.8) 27	9.36±0.20 (9.1- 9.9) 19	9.40±0.27 (8.8-10.0) 41
Mastoid breadth	♂	9.15±0.13 (9.0- 9.4) 12	8.99±0.23 (8.7- 9.4) 19	8.94±0.24 (8.5- 9.4) 47
	♀	9.14±0.16 (8.7- 9.5) 30	8.97±0.12 (8.8- 9.2) 21	8.96±0.21 (8.5- 9.5) 43
Interorbital breadth	♂	4.33±0.07 (4.2- 4.4) 12	4.01±0.13 (3.8- 4.3) 19	4.04±0.15 (3.8- 4.3) 47
	♀	4.24±0.12 (3.9- 4.4) 30	4.02±0.14 (3.8- 4.3) 21	4.08±0.15 (3.8- 4.3) 44
Length of maxillary toothrow	♂	6.89±0.20 (6.5- 7.2) 12	6.76±0.15 (6.5- 7.0) 18	6.79±0.19 (6.3- 7.1) 47
	♀	6.99±0.18 (6.7- 7.5) 30	6.79±0.13 (6.5- 7.0) 21	6.94±0.15 (6.6- 7.2) 44
Greatest width across molars	♂	5.67±0.13 (5.4- 5.9) 12	5.45±0.17 (5.1- 5.7) 18	5.46±0.17 (4.8- 5.8) 47
	♀	5.66±0.10 (5.4- 5.8) 30	5.46±0.19 (5.2- 5.6) 20	5.56±0.17 (5.3- 6.0) 44

mi. SE San Blas, 1 (KU). SINALOA: 20 km. N, 5 km. E Badiraquato, 1800 ft., 2 (KU); Santa Lucía, 3600 ft., 2 (KU).

Specimens (131) of *G. c. commissarisi* used in comparisons and in Table 1 are from the localities that follow. CHIAPAS: 15 km. ESE Tonalá, 3 (LACM); 10 km. SE Tonalá, 20 (LACM); 8 mi. SE Tonalá, Finca Ocuilapa, *ca.* 100 ft., 6 (3 LACM, 3 UA); 9 mi. SE (and then) 8 mi. NE Tonalá, 1 (LACM); 12.5 km. SE Tonalá, 8 (LACM); 21 km. SE Tonalá, 2 (LACM). COSTA RICA: *Alajuela*: Los Chiles, 2 (LACM); Playuela, 1 (LACM). *Guanacaste*: 7 mi. SW Filadelphia, 7 (KU); Finca la Pacifica, 4 mi. NW Cañas, 1 (MSB). *Heredia*: Puerto Viejo, 1 (KU). *Limón*: Finca la Lola, 2 (LACM). *Puntarenas*: Boca de Río Barranca, 1 (LACM); Monteverde, 2 (LACM). PANAMA: *Bocas del Toro*: Almirante, 24 (USNM); Boca del Drago, 1 (USNM); Cayo Agua, Puerta Norte, 4 (USNM); Sibube, 1 (USNM). *Canal Zone*: Buena Vista Peninsula, 1.75 km. NNW Frijoles, 1 (USNM). *Chiriquí*: 1 mi. E Cuestra de Piedra, 2800 ft., 3 (USNM); San Vicente, 1800 ft., 1 (USNM). *Coclé*: Santa Clara, 1 (USNM). *Darién*: Jaqué, 7 (USNM); Tacarcuna Village Camp, 3200 ft., 9 (USNM). *Panamá*: Cerro Azul, 13 (USNM). *San Blas*: Armila, Quebrada Venado, 7 (USNM); Mandinga, 2 (USNM).

For the record, the northernmost marginal localities of *G. c. commissarisi* known to us are: Mirador, Veracruz (1 USNM); 8 km. S Solusuchiapa, *ca.* 400 ft., Chiapas (3 LACM); Lubaantun, Toledo, Belize (1 FMNH); Santiago Lachiquirí (2 AMNH) and 6 mi. S Matias Romero, Río Grande (1 USNM), Oaxaca.

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RESOLVING A PHYLOGENY WITH MULTIPLE DATA SETS: A SYSTEMATIC STUDY OF PHYLLOSTOMOID BATS

Michael L. Arnold, Rodney L. Honeycutt, Robert J. Baker,
Vincent M. Sarich, and J. Knox Jones, Jr.

All comparative biological data (in this study morphological, chromosomal, electrophoretic, and immunological) ultimately must be interpretable within a specific framework—the actual phylogeny of the set of organisms under study. An obvious corollary is that each data set should contribute toward the delineation of that phylogeny. The quality and magnitude of contribution, of course, will vary with the nature of the data set and its mode of evolution, because two conditions are necessary. First, a change must have occurred along the lineage under study and second, evidence of change must be observable.

In this study, we were concerned with delineating phylogenetic relationships among the three families of New World bats currently placed in the superfamily Phyllostomoidea—Noctilionidae (one genus, two species), the Mormoopidae (two genera, eight species), and the Phyllostomidae (some 49 genera and approximately 139 species). In addition, we have examined intrafamilial associations in the Noctilionidae and the Mormoopidae.

The genera *Mormoops* and *Pteronotus* classically have been placed either in the family Mormoopidae or (formerly) in the subfamily Chilonycterinae within the family Phyllostomidae. The systematic association of *Mormoops* with *Pteronotus*, suggesting a shared common ancestor for these genera following their separation from all other taxa in the superfamily, has been recognized since the work of Dobson (1875). *Noctilio*, on the other hand, clearly has presented more of a problem to chiropteran systematists. Some workers have associated *Noctilio* with the Emballonuroidea (Dobson, 1875; Trouessart, 1897; Miller, 1907; Simpson, 1945), whereas others (Winge, 1892; Smith, 1972; Patton and Baker, 1978) have indicated a mormoopid-phyllostomid association for these bats.

Chromosomal change between the Mormoopidae and Noctilionidae constitutes the least amount of divergence thus far documented between two mammalian families (Patton and Baker, 1978). Chromosomal data have been interpreted as supporting a common ancestry for the two families (five synapomorphic elements present) and for the two mormoopid genera (one synapomorphic element present—Patton and Baker, 1978), with two rearrangements distinguishing *Mormoops* from *Pteronotus* (Baker and Bickham, 1980).

In order to understand better the evolution of the superfamily Phyllostomoidea, we have reviewed the resolving power and systematic value of classical comparative anatomy, karyology (using G- and C-banding techniques), electrophoresis of various proteins, and albumin immunology. Furthermore, we have evaluated the extent to which each of the above analyses contributes to the delineation of an internally consistent phylogeny.

MATERIALS AND METHODS

Electrophoretic Analyses

All samples were assayed for 18 isozymes. The enzyme and protein systems were malate dehydrogenase-1 and 2 (Mdh-1,2), phosphoglucomutase-1 and 2 (Pgm-1,2), lactate dehydrogenase-1 and 2 (Ldh-1,2), isocitrate dehydrogenase-1 and 2 (Idh-1,2), α-glycerophosphate dehydrogenase (α-Gpd), leucine aminopeptidase (Lap), peptidase (Pep), phosphoglucose isomerase-1 and 2 (Pgi-1,2), glutamate oxalate transaminase-1 and 2 (Got-1,2), indophenol oxidase (Ipo), albumin (Alb), and hemoglobin (Hb). Tissue preparations, staining procedures, and enzyme designations followed those of Selander *et al.* (1971).

For examination of electrophoretic data, populations (see list of specimens examined for numbered localities) 1-7 (*Pteronotus parnellii*), 8-9 (*Pteronotus davyi*), 12-13 (*Pteronotus personatus*), 15-16 (*Mormoops megalophylla*), and 18-20 (*Noctilio leporinus*) were grouped according to species. A cladistic analysis was performed on the data set by using the electromorphs as independent character states (Hennig, 1966). The two species of *Noctilio* represented an outgroup comparison for *Pteronotus* and *Mormoops* in the electrophoretic study. Any allele present in both *Noctilio* and species of *Mormoops* and *Pteronotus* was considered primitive for the two families. Further resolution of phylogenetic relationships, based on electrophoretic data, was made possible by using the isozyme systems for which no primitive allozyme was distinguishable from the outgroup comparison. This involved examination of the polarity of allozymic variation, with the assumption that the most common electromorph was primitive for the mormoopid-noctilionid clade and that all other variants were derived. The results from the use of this technique did not involve the rearrangement of any relationships defined by the outgroup process; rather, they further refined relationships involving previously undefined lineages.

Immunological Analyses

The albumins of *Mormoops megalophylla, Pteronotus parnellii,* and *Noctilio leporinus* were purified according to the techniques of Cronin and Sarich (1975). Antisera to these albumins were prepared in rabbits (three to four Dutch Belted rabbits per albumin according to the schedule of Sarich, 1969), and each individual antiserum then was titered using microcomplement fixation (MC'F) and pooled in reciprocal proportion to its titer (Sarich and Wilson, 1966). Additionally, two antisera pools to the albumins of phyllostomid bat genera (*Macrotus, Vampyrum, Glossophaga, Carollia,* and *Desmodus*) and pteropoid bat genera (*Syconycteris, Pteropus, Dobsonia, Nyctimene,* and *Paranyctimene*) were used to provide estimates of the amounts of albumin change along the *Mormoops, Pteronotus,* and *Noctilio* lineages, as well as to test for relationships to the phyllostomids. All antigens used for cross-reactions with the different antisera were extracted from samples of whole serum or tissue diluents.

Immunological cross-reactions (antigen-antibody reactions) for all comparisons were measured by the quantitative precipitin technique employed by Sarich and Wilson (1966) and Prager and Wilson (1971). The degree of cross-reaction was expressed quantitatively as albumin immunological distance units (AID), with one unit being approximately equivalent to one amino acid substitution (Prager and Wilson, 1971; Maxson and Wilson, 1974).

Specimens Examined

Specimens used in this study were collected at the following localities: *Pteronotus parnellii.*—1) 1 km. N Mérida, Yucatán, México, 2 females; 2) Guatopo

National Park, Santa Crucita Campground, Venezuela, 2 females, 1 male; 3) 1 mi. N El Dorado, Sinaloa, México, 3 males; 4) 2 mi. NE Rosario, Sinaloa, México, 1 male; 5) 0.4 mi. E Hwy. 15 on road to Acaponeta, Nayarit, México, 1 male; 6) 24.1 mi. N Río La Unión on Hwy. 200, Guerrero, México, 1 male; 7) 0.2 mi. E Watermount, Jamaica, 16 females, 5 males; *Pteronotus davyi.*—8) 15 km. N Altagracia de Orituco, Guarico, Venezuela, 1 female; 9) Tanetane, St. John Parish, Dominica, 7 females, 10 males; *Pteronotus macleayii.*—10) St. Clair Cave, St. Catherine Parish, Jamaica, 15 females, 5 males; *Pteronotus quadridens.*—11) St. Clair Cave, St. Catherine Parish, Jamaica, 11 females, 10 males; *Pteronotus personatus.*—12) Tehuantepec, Oaxaca, México, 5 males; 13) El Fuerte, Sinaloa, México, 1 male; *Mormoops blainvillii.*—14) St. Clair Cave, St. Catherine Parish, Jamaica, 20 males; *Mormoops megalophylla.*—15) 24.1 mi. N Río La Unión on Hwy. 200, Guerrero, México, 1 female; 16) 8.2 mi. S Piña Blanca on Hwy. 120, Querétaro, México, 2 males; *Noctilio albiventris.*—17) 15 km. N Altagracia de Orituco, Guarico, Venezuela, 1 female, 1 male; *Noctilio leporinus.*—18) 0.2 mi. E Watermount, St. Catherine Parish, Jamaica, 5 females, 3 males; 19) mouth of Belham River, St. Anthony, Montserrat, 3 females, 4 males; 20) 1 mi. above mouth of Layou River, St. Joseph Parish, Dominica, 1 female.

RESULTS AND DISCUSSION

Electrophoretic Analyses

Only one isozyme (Lap) was monomorphic for all populations (Table 1). Nine of the remaining 17 isozyme systems yielded information concerning primitive and derived conditions using the outgroup criteria. The cladogram represented by Fig. 1 was produced by first using the data from these systems and then further resolving relationships based on the remaining allelic data as discussed in the section on methods. Allozymes present in the internodes (for example, Got-1^{156}) are synapomorphic for the species located above the internode, whereas allozymic characters located on branches ending in a single species (for example, Idh-1^{100}) are considered autapomorphies for that species.

Several phylogenetic relationships are suggested from the cladistical analysis of electrophoretic data (Fig. 1). First, a clade composed of the five *Pteronotus* species is defined by four synapomorphic electromorphs. Within that assemblage, *P. parnellii* is separated from the other four species by the Idh-1^{133} and Got-1^{156} allozymes.

The two species of *Mormoops* and the two of *Noctilio* are united by three and seven shared characters, respectively, with all of these electromorphs belonging to loci for which the outgroup criteria failed to discriminate primitive and derived conditions.

TABLE 1. *Allozyme data for the 20 populations of mormoopid and noctilionid bats (see text for identification of numbered populations). The mobility of the most frequent allozyme in population 2 was arbitrarily designated 100 with all other allozymes being designated relative to this electromorph. A negative (−) sign indicates a cathodal mobility of the allozymes, whereas the lack of any sign indicates anodal mobility.*

	Population										
Isozyme	1	2-7	8-9	10	11	12	13	14	15-16	17	18-20
Mdh-1	100	100	100	100	100	100	100	34	44	138	138
Mdh-2	−100	−100	−107	−100	−100	−100	−100	−100	−100	−89	−89
Pgm-1	100	100(0.98) 30(0.02)	100	100	100	153	153	153	153	153	153
Pgm-2	−100	−100	−100	−129	−100	−100	−100	−100	−100	−100	−100
Ldh-1	100	100	100	100	100	100	100	126	82	147	147
Ldh-2	−100	−100	−100	−100	−89	−100	−100	100	−100	−100	−100
Idh-1	100	100	133	133(0.42) 171(0.58)	133	133	133(0.50) 95(0.50)	114	164	114	114
Idh-2	−100	−100	−62	−38	−108	−100	−100	−88	−38	−38	−38
α-Gpd	100	100	48	48	48	100	100	66	66	145	117
Pep	100	100	100	100	84	78	78	130	122	182	182
Pgi-1	83	100	140	140	157	140	140	187	187	180	180
Pgi-2	100	100	100	120	100	140	140	240	240	80	80
Got-1	100	100	156	156	156	156	156	100	72	100	200
Got-2	−100	−100	−100	−73	−100	−100	−100	−100	−68	−100	−55
Ipo	−100	−100	−100	−100	−100	−100	−100	−100	−100	−31	−31
Alb	100	100	96	100	89	100	100	117	112	112	112
Hb	−100	−100	−100	−100	−100	−100	−100	−100	−67	−100	−100
Lap	100	100	100	100	100	100	100	100	100	100	100

Morphological Analyses

Smith (1972) analyzed the morphological relationships between the families Mormoopidae, Noctilionidae, and Phyllostomidae as well as the inter- and intrageneric relationships of mormoopid taxa. Although Smith's study was basically phenetic in its approach, he did evaluate a large array of qualitative characteristics, not only for the Phyllostomoidea but also for other New World Chiroptera. This set of data is unique for bats in that it provides an adequate base for cladistic analysis. Fig. 2 represents our interpretation of these qualitative characters, a description of which appears in the legend. In deriving the cladogram, we assumed that emballonuroids represent a valid outgroup.

The resolved phylogentic tree (Fig. 2) presents several salient features. The families Phyllostomidae, Mormoopidae, and Noctilionidae share several synapomorphies and represent a unified clade, as suggested by Smith (1972). However, a closer association of the Noctilionidae to the Mormoopidae than to the Phyllostomidae is not demonstrable. Although the Mormoopidae and Noctilionidae share a single derived character, a synapomorphic ele-

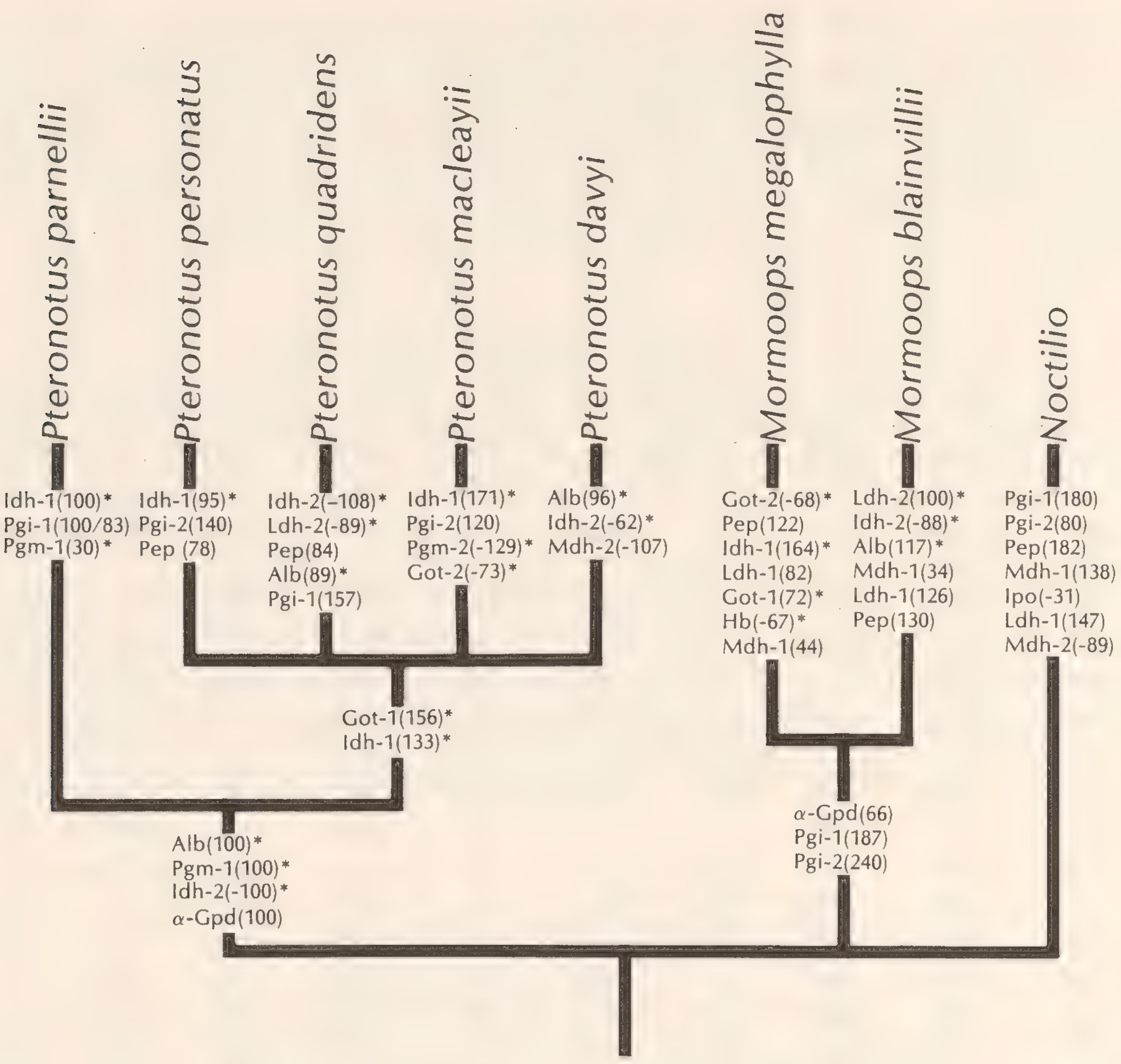

FIG. 1.—Cladogram based on allozymic variants. Allozymes denoted by asterisk were resolved using the outgroup method. See text for identification of abbreviations.

ment also is present between the families Phyllostomidae and Mormoopidae. One synapomorphy places the genera *Mormoops* and *Pteronotus* together; another (shape of tragus) separates *P. parnellii* from its congeners, with the other four species of *Pteronotus* forming an unresolved tetrotomy. One and three synapomorphic characters, respectively, unites the species of *Noctilio* and *Mormoops.*

Karyotypic Analyses

Chromosomal data as presented by Patton and Baker (1978) and Baker and Bickham (1980) add additional resolution to phylogenetic relationships within the Phyllostomoidea (Fig. 3). The primitive karyotype for the superfamily, as proposed by Patton and Baker (1978), consists of a $2n=46$ and $FN=60$, essentially the karyotype of the phyllostomid species *Macrotus waterhousii.* Based on the assumption that the $2n=46$, $FN=60$ karyotype is primitive for the Phyllostomoidea, the families Noctilionidae and Mormoopidae are linked by five synapomorphies (Robertsonian fusions). Patton and Baker (1978), using the rule of parsimony, indicated that the

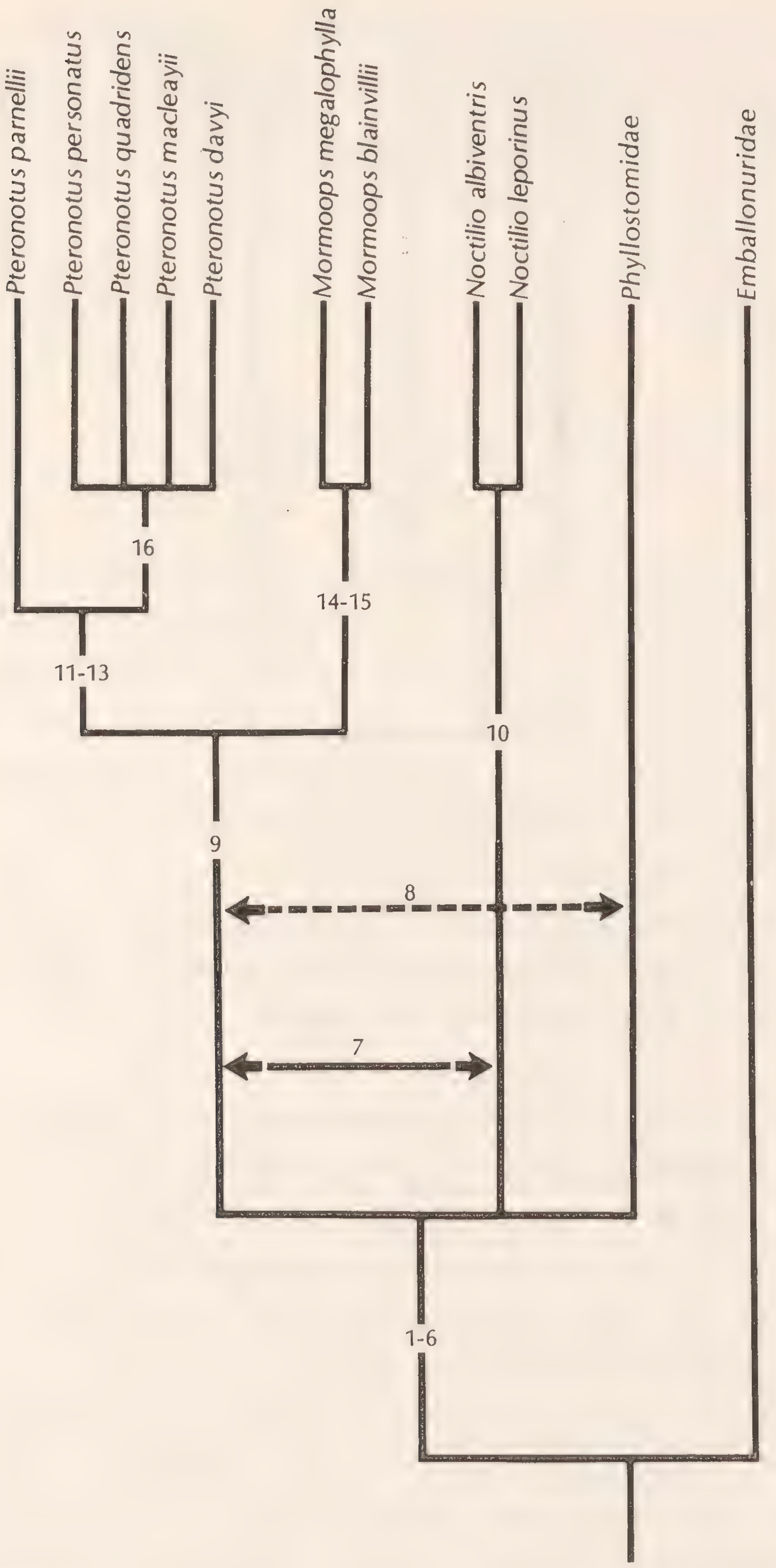

Fig. 2.—Cladogram based on morphological characters examined by Smith (1972): **1**, Premaxillary bones complete and fused to maxillary and palatine bones; **2**, Os penis absent; **3**, Marked sella turcica; **4**, Foramen ovale similarly situated; **5**, Wartlike bumps and ridges on lower lip; **6**, Lanceolate tragus; **7**, Capitulum and trochlea lie in an intermediate position; **8**, Supraglenoid fossa well developed; **9**, Trochanter on proximal end of femur not distinct; **10**, Tragus slender, pinnately-lobed; **11**, Medial process moderate in length; **12**, Capitulum and radius form "tongue and groove"; central part of capitulum larger; **13**, Tragus with secondary fold greatly increased in size and forming major part of structure; **14**, Medial process shortened; **15**, Well-developed tragus fold; **16**, Well-developed secondary tragus fold.

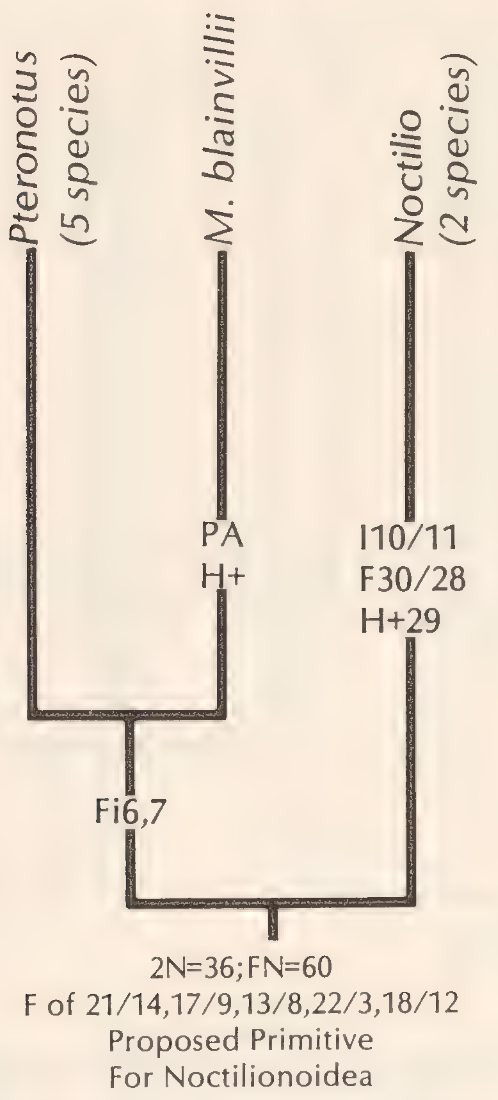

FIG. 3.—Cladogram based on chromosomal data from studies by Patton and Baker (1978), and Baker and Bickham (1980): F=fusion, H+=heterochromatic addition, I=inversion, PA=paracentric inversion.

fusion events probably were synapomorphies inasmuch as several more events, including fissions preceded by several fusions, would have to be invoked to explain a noctilionid-mormoopid-like karyotype as primitive. A cladistic analysis to determine a primitive karyotype for the Phyllostomoidea cannot be performed at this time because homologous elements have not been identified with appropriate outgroups. Mormoopid and noctilionid species differ by four rearrangements (Patton and Baker, 1978)—a fission event in the mormoopids (synapomorphic for *Mormoops* and *Pteronotus*) and an inversion, a fusion event, and a heterochromatic addition in the noctilionids (synapomorphic for the two *Noctilio* species). Additionally, *Mormoops blainvillii* differs from the species of *Pteronotus* by a paracentric inversion and a heterochromatic addition (Baker and Bickham, 1980).

Immunological Analyses

A salient feature of almost all phyllostomoid albumins is their immunological distinctiveness relative to those of other bats. The assumption of microchiropteran monophylly or the use of phylogenetic analyses involving nonbat reference species (Sarich, unpublished data) leads to the conclusion that an event producing

TABLE 2.—*Albumin immunological distance values for mormoopid and noctilionid species. The Phyllostomidae sample is a mixed outgroup consisting of* Macrotus, Vampyrum, Glossophaga, Carollia, *and* Desmodus. *The Pteropodidae sample consists of* Syconycteris, Pteropus, Dobsonia, Nyctimene, *and* Paranyctimene.

Taxon	*M.m.*	*P.p.*	*N.l.*	Ph.
Mormoops megalophylla	0	95	146	87
Pteronotus parnellii		0	150	80
Noctilio leporinus			0	135
Phyllostomidae				0
Pteropodidae	140	178	180	172

the antigenic equivalent of 30 to 40 units of albumin immunological distance must have occurred early in phyllostomoid history (Table 2, Fig. 4). Thus, this event has provided an effective phenetic marker that positions a wide variety of New World bats into a single clade. It also would appear that such an event has caused a relative rate destabilization for subsequent albumin evolution in the group (at least as it is assessed immunologically). There is appreciably more variation in observed amounts of change along different lineages than has been demonstrated in any other vertebrate group (Honeycutt and Sarich, unpublished data). It thus is fair to point out that the "molecular clock" concept never would have been formulated on the basis of a study of phyllostomoid albumin evolution. This does not, however, affect our cladistic analysis, as the data for phyllostomoid bats apportion into additive phylogenies at least as well as do those for any other group for which similar information is available. For example, the *F* value (Prager and Wilson, 1978) for the input-output comparisons involving 16 phyllostomid albumins and antisera to them is less than 5 per cent (Honeycutt and Sarich, unpublished data).

As systematists, we find it disturbing that the cladistical analysis of data from albumins of *Mormoops* are not consistent with the results of similar analyses of morphological and chromosomal data. *Mormoops*, *Pteronotus*, and various phyllostomid albumins are more or less equidistant from one another. Indeed, if anything, the albumins of the two mormoopid genera are, on the average, somewhat more distant from each other than either is from albumins of the phyllostomids. However, we would have expected, given the usual association of *Mormoops* and *Pteronotus* on the basis of anatomical similarities, to find that their albumins had changed to a greater degree than those of the phyllostomids. Otherwise, the albumin data would not be readily interpretable within the generally agreed upon framework that

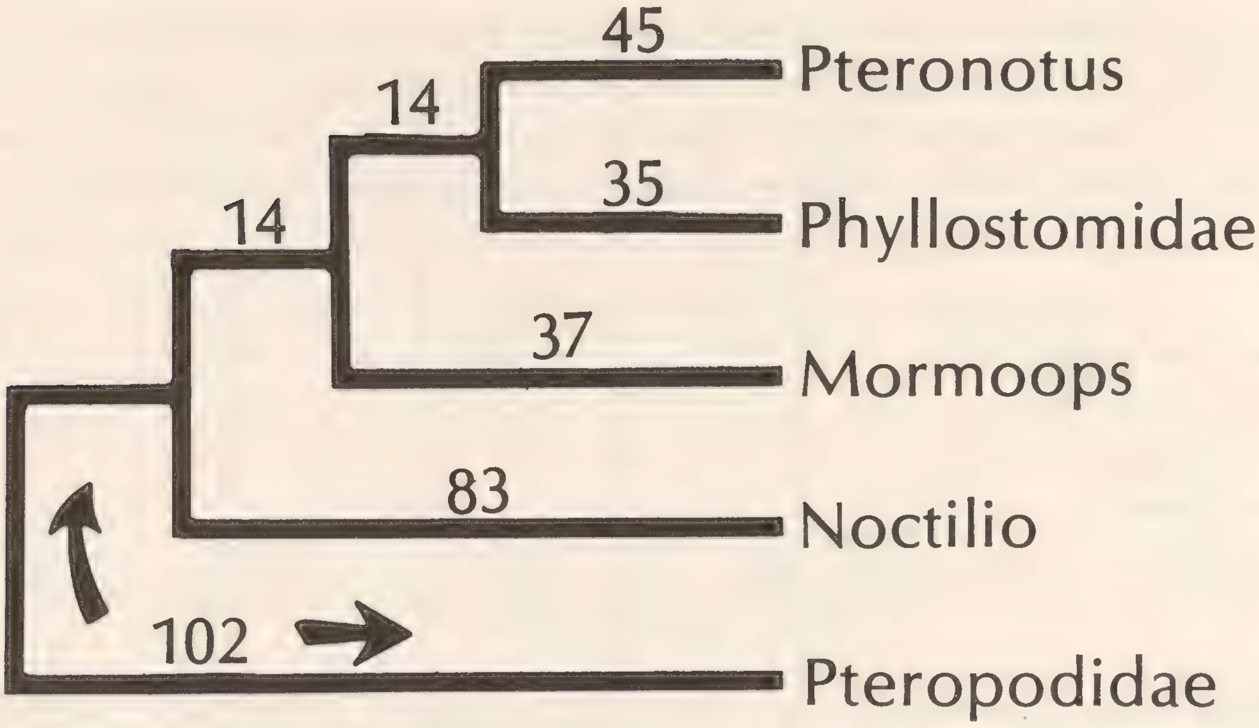

FIG. 4.—Cladogram of the Phyllostomoidea lineages based on the albumin immunological distances of Table 2. The numbers along the lines represent the amount of albumin change allocated to a particular lineage. The Family Pteropodidae is used as an outside reference point to root the tree and apportion the amounts of change among lineages.

represents mormoopids as a derived unit relative to other bats. Yet we find that the least-changed albumin in this set is that of *Mormoops megalophylla,* at a distance of 140 units from our pteropodid reference set, whereas *Pteronotus parnellii* is 178 and the phyllostomid mean is 172 (Table 2). These data may be explained most parsimoniously by suggesting that the phyllostomids and *Pteronotus* shared a common ancestor (separate from *Mormoops*) in which there was an albumin change of approximately 30 or so AID units (Fig. 4)—in other words, a second event of similar magnitude as that proposed to have occurred in the common ancestral stock of all phyllostomoid bats.

Noctilio is still another problem immunologically. Its albumin is divergent in the same way as that of other phyllostomoids, being some 180 units from those of the pteropodids (Table 2). It also is quite different from those of other phyllostomoid lineages with which we are concerned. The distances separating *Noctilio* from *Pteronotus, Mormoops,* and an assortment of phyllostomids are 150, 146, and 135 units, respectively (Table 2). The cladistic implications of these data are not unequivocal. For example, the apportionment of the *Noctilio*-phyllostomid distance of 135 units, using the pteropodid information, would suggest a *Noctilio* separation somewhere along the common phyllostomoid lineage to which we have allocated a singular conformation-altering mutation (Fig. 4). Subsequent to that separation, it is then evident that this "event" was completed in a somewhat different fashion along the *Noctilio* line relative to what happened along the *Pteronotus*-phyllostomid line, thus resulting in a markedly divergent albumin.

Albumin Irregularities

Over the last 15 years, extensive evidence has been developed that documents the generally time-dependent nature of immunologically assessed albumin evolution. However, significant individual departures from this pattern do exist in that a few lineages among many have accumulated change at a rate significantly greater or less than the average. Examples are *Aotus, Caluromys, Marmosa,* and *Ursus* on the slow side, and *Rousettus* and *Phaner* on the fast side (Sarich, 1969; Cronin and Sarich; Maxson *et al.*, 1975). Of course, such a lineage ultimately could develop into a major adaptive radiation leading to a large clade, all the individual lines of which might appear removed from clocklike behavior; one such instance already has been reported (Cronin and Sarich, 1975). In that particular case, it appears that at some time along the ancestral anthropoid lineage, subsequent to the anthropoid-prosimian split, about 25 to 30 units of change in excess of the average accumulated. Almost all anthropoid albumins thus appear to be changed to a greater degree than do those of most prosimians. Although this could be regarded simply as twice the usual rate of change over the period of time involved (about 30 million years), the rate being normal before and after, it is appreciably easier to envision it as resulting from a single mutation that somehow altered the conformation of the albumin surface so as to be the antigenic equivalent of many individual amino acid substitutions.

There is excellent evidence that the number of differences in the surface amino acid sequence between two native proteins can be closely approximated by quantitative immunological comparisons (reviewed in Wilson *et al.*, 1977), although alterations of the three-dimensional structure can have drastic effects. One can imagine, therefore, a single internal amino acid substitution (perhaps involving a cysteine and the subsequent relocation of one or more disulfide bridges) that could have a similar effect on the three-dimensional protein structure on a reduced scale. One also might interject a cautionary note here concerning the possible nonequivalence of immunological distances derived from conformational changes and those derived from the accumulation of single amino acid substitutions. We include this as a final note for consideration of albumin evolution in phyllostomoid bats, where more than the usual number of interpretive problems exist.

Character State Evolution and the Derivation of Phylogenies

As witnessed by a continuing list of authors (Mickevich and Johnson, 1976; Schnell *et al.*, 1978; Turner, 1974), the derivation of a consistent (that is, congruent) phylogeny using different character states is, to say the least, complicated. Is a similar method of analysis (cladistics) the key to deriving congruent phylogenies? Consistency seems achievable if one adequately can interpret patterns of character state divergence in terms of a similar method of analysis that potentially can detect differential rates of change, degree of homoplasy, and primitive (as opposed to derived) conditions. The cladistical method seems appropo; however, regardless of the method of analysis, certain limitations inherent to a particular type of character may limit congruence (Fig. 5). In our data sets, limitations for different character states can be categorized as follows: 1) In terms of morphology, chiropteran systematics is still at a stage where evolutionary relationships are based mainly on a "gestalt," due in part to the lack of a fossil record. An appropriate quantitative approach (void of size relationships) to morphological relationships within chiropterans does not exist. The qualitative approach used in our study does support the phyllostomoid superfamilial association; however, the associations among the three families as well as those between *Mormoops* and *Pteronotus* are much more tentative (Figs. 2 and 5). 2) The electrophoretic approach is limited by inability to resolve synapomorphic character states among the genera *Mormoops, Pteronotus,* and *Noctilio* (Fig. 1). 3) The chromosomal approach is limited because of our current inability to decipher chromosomal homologies between superfamilies and thus to determine conclusively (without the rule of parsimony) primitive conditions at superfamilial levels (Figs. 3 and 5). 4) Phylogenetic associations such as those implied with albumin immunological data are clearly more accurate in cases where divergence can be correlated to surface amino acid substitutions. Structural changes of the albumin molecule only can be inferred and at this stage in scientific investigations are not usually verifiable (Table 2).

The inconsistent resolving power associated with a given suite of characters indicates that the best phylogeny generated from different types of characters need not reflect total congruence. Rather, an alternate consideration would be one of compatibility.

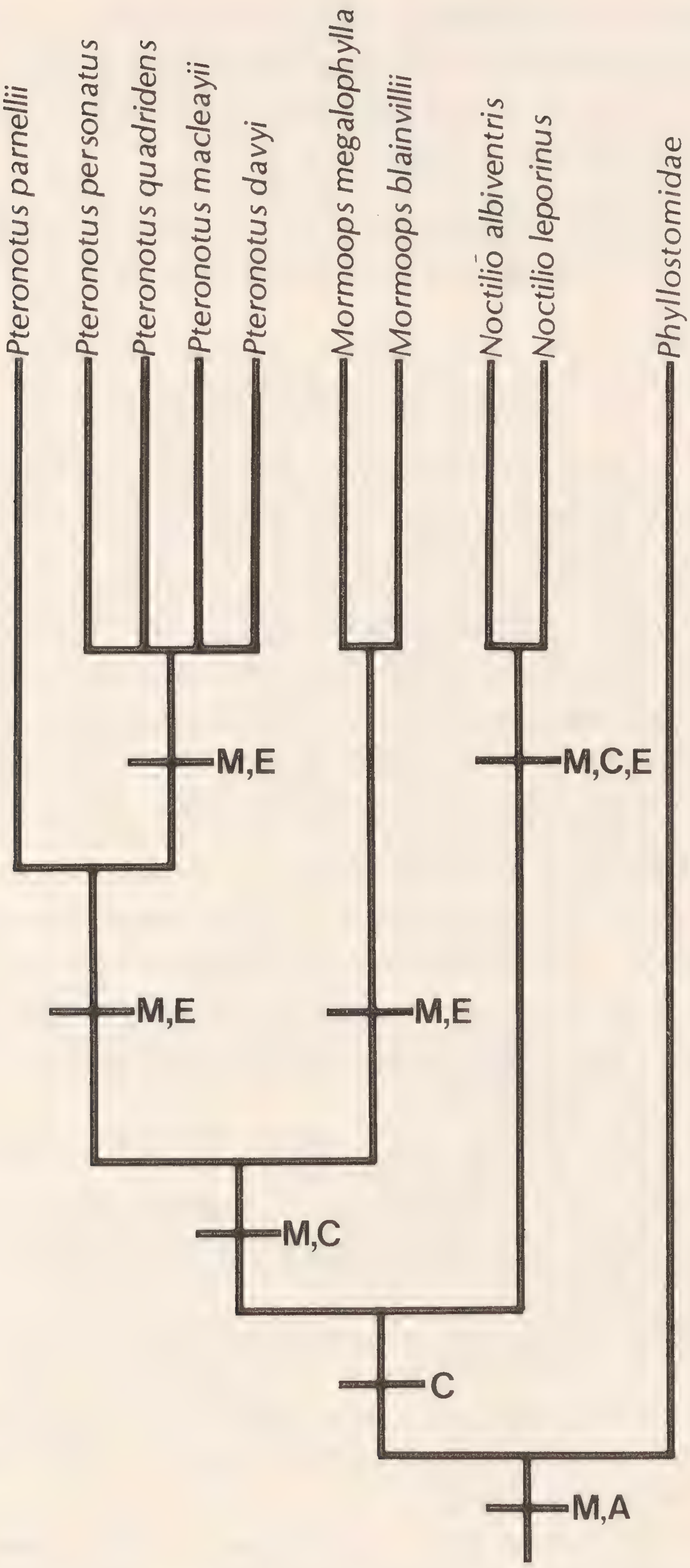

FIG. 5.—Composite cladogram indicating the levels of resolution of each of the character sets used: A=albumin, C=chromosomal, E=electrophoretic, and M=morphological.

Every character does not have to resolve the same branching sequences at different evolutionary levels; however, all characters should lead to maximum compatibility. The failure of certain characters to resolve branching sequences at a given level then can be regarded as neutral insofar as determination of a consistent phylogeny. Incompatibility occurs only when different characters reveal conflicting branching sequences. One is then forced to assess this incompatibility in terms of the characters used and the inconsistencies and limitations associated with those characters (see immunological discussion).

Our study supports the conclusion that a complex phylogeny can be resolved best by the use of multiple, differentially resolving character sets.

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COMMENTS ON THE STATUS OF MUSONYCTERIS HARRISONI (CHIROPTERA: PHYLLOSTOMIDAE)

WM. DAVID WEBSTER, LYNN W. ROBBINS,
R. LAURIE ROBBINS, AND ROBERT J. BAKER

Musonycteris harrisoni is a monotypic glossophagine known only from xeric scrub forests in western México (Jalisco southeastward to Guerrero). Although the systematic relationships among many glossophagines are uncertain because of the apparent convergence associated with nectivory, *Musonycteris* appears to be most closely related to *Choeronycteris mexicana.* In the original description of *Musonycteris,* Schaldach and McLaughlin (1960) allied it morphologically with *Choeronycteris* and distinguished between the two using differences in the basicranium and in rostral proportions. However, because differences in rostral proportions between two species, *Choeroniscus godmani* and *C. periosus,* of another genus in the subfamily exceeded those between *Musonycteris* and *Choeronycteris,* Handley (1966) considered *Musonycteris* to be congeneric with *Choeronycteris* so as not "to obscure relationships in this segment of the Glossophaginae." Handley further concluded that *Hylonycteris, Scleronycteris,* and *Lichonycteris,* although less specialized for nectivory, also were related to *Choeroniscus* and *Choeronycteris.* Phillips (1971) regarded *Musonycteris* and *Choeronycteris* as distinct genera based on basicranial differences and the expanded metastyle of M^3 of *Musonycteris,* but agreed with Handley concerning the systematic affinities of the other genera.

The karyotypic relationships of these bats were discussed by Baker (1967, 1979) and Gardner (1977). *Choeronycteris* ($2n=16$, FN=24, plate 22 of Baker, 1979) and *Hylonycteris* ($2n=16$, FN=24, plate 24 of Baker, 1979) appear to have karyotypes that are similar and unique among phyllostomids. Baker (1979) attributed this similarity to a common ancestor with a diploid number of 16 and fundamental number of 24, whereas Gardner (1977) thought the two species independently converged from a $2n=32$, FN=30 progenitor to the present karyotype derived by a series of fusions.

The species of *Choeroniscus* thus far examined have diploid numbers of 18 to 19 or 20 and fundamental numbers of 32 or 36. Although Baker (1967) noted the similarity in the standard karyotype and sex determining mechanisms (XX/XY_1Y_2) in *Choeroniscus* and *Carollia* (subfamily Carolliinae), Stock (1975) found essentially no G or C-band autosomal homologies in those genera. Patton and Gardner (1971) also suggested that a common evolutionary origin of the multiple sex chromosomes of *Carollia* and *Choeroniscus* was doubtful. It also should be noted that the five males of *Choeroniscus godmani* thus far examined had a $2n=19$, whereas the three females had a $2n=20$, suggesting a system in which the Y has been translocated to an autosome rather than an autosome being translocated to the X, as has occurred in *Carollia*. A note of caution, however, should be considered, because the males (from Chiapas) and females (from Costa Rica and Honduras) were taken from separate geographic localities, and different cytotypes might be involved. *Lichonycteris* ($2n=24$, FN=44) is karyotypically distinct among glossophagines; Gardner (1977) assumed it was derived from a $2n=32$, FN=30 progenitor primarily by pericentric inversions. The karyotypes of *Scleronycteris* and *Platalina* are unknown, and that of *Musonycteris* is discussed below.

The autosomal karyotypes of two *Musonycteris harrisoni* (TTU 36153, and 36433, both adult males) from 2 mi. NW Tomatlán, Jalisco, consisted of one large pair of submetacentrics, one large pair of subtelocentrics, a medium pair each of subtelocentrics and submetacentrics, and three small pairs of acrocentrics (Fig. 1). The sex chromosomes are small heteromorphic metacentrics. Thus, the data indicate that the karyotype of *Musonycteris* ($2n=16$, FN=22) resembles those of *Choeronycteris* and *Hylonycteris*, but differs autosomally from both in possessing three small pairs of acrocentrics (rather than two). The X appears to be biarmed and metacentric in *Choeronycteris* (plate 22 of Baker, 1979), *Hylonycteris* (plate 24 of Baker, 1979), and *Musonycteris* (Fig. 1). The Y is biarmed in both *Choeronycteris* and *Musonycteris*. The Y of

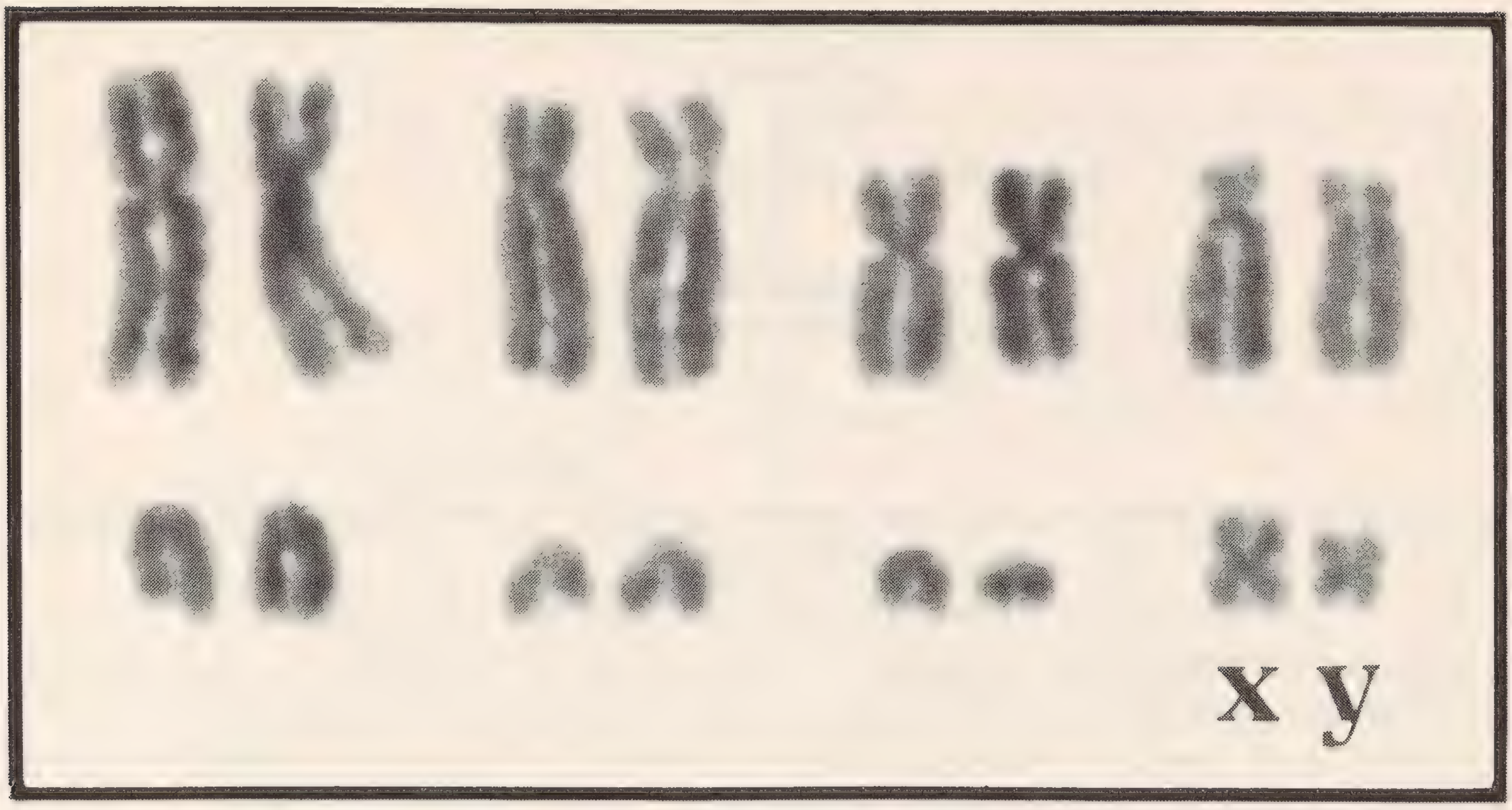

FIG. 1.—Karyotype of a male *Musonycteris harrisoni* from Jalisco, México.

Hylonycteris (TTU 36152, adult male from 3 km. E Teapa, Grutas de Cocona, Tabasco) is approximately half the size of the X but has extremely reduced arms above the centromere.

The following points are critical in evaluating the evolutionary relationships of *Musonycteris* as indicated by karyotypes. A synthesis of G-banded chromosomal, albumin immunological, and electrophoretic data suggests that a $2n=32$, FN=60 karyotype such as that found in *Glossophaga* was primitive for the clade of the Glossophaginae containing *Glossophaga, Monophyllus, Leptonycteris, Anoura, Choeronycteris,* and *Hylonycteris* (Baker *et al.*, 1981). Therefore, the most parsimonious conclusion is that taxa with morphologically similar $2n=16$ karyotypes possess a highly derived chromosomal phenotype, most features of which were established in the common ancestor for the three genera (*Choeronycteris, Musonycteris,* and *Hylonycteris*). However, standard karyotypes of the three are not identical, and a schematic representation of how the karyotypes of each might be modified into those of the other two is shown in Fig. 2. The significant point to be derived from this diagram is that no data from standard karyotypes document that *Musonycteris* and *Choeronycteris* are more closely related to each other than either is to *Hylonycteris*. It is probable that the differences noted in those genera do not result from heterochromatic additions, a rare event in phyllostomid bats (see Baker and Bickham, 1980: table 1).

Morphological and karyotypic similarities indicate that *Musonycteris* and *Choeronycteris* are closely related, but we are reluc-

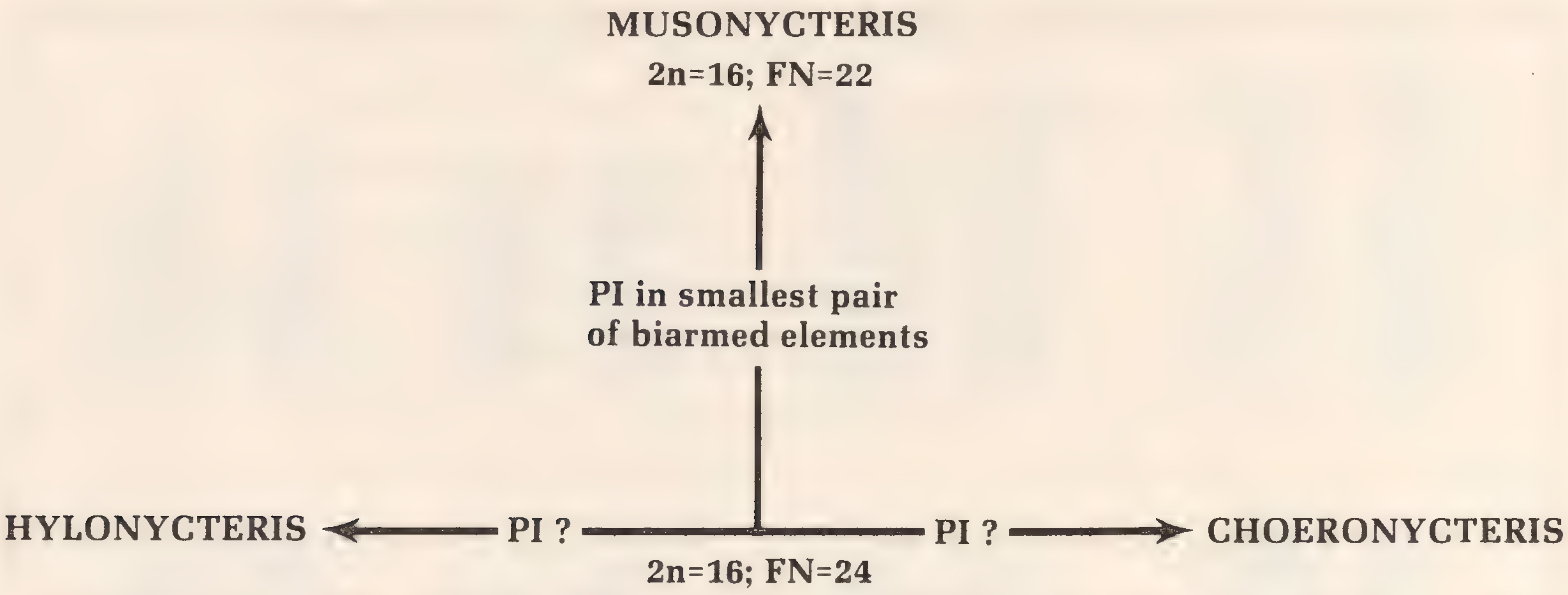

FIG. 2.—The most parsimonious path of change to explain differences in autosomes of *Choeronycteris*, *Musonycteris*, and *Hylonycteris*. The pair of autosomes possibly inverted (PI) in the lineages of *Hylonycteris* and *Choeronycteris* is the second pair of row 2 in plates 22 and 24 of Baker (1979). Also, it should be noted that the two pairs of acrocentric autosomes in *Choeronycteris* are unequal in size, whereas they are equal in *Hylonycteris*.

tant to consider them congeric for several reasons. Clearly, the well-developed basisphenoid ridge, smaller braincase, narrower and more elongate (but domed) rostrum, expanded metastyle on M^3, and reduced depth of the mandibular ramus in *Musonycteris* separate it from *Choeronycteris*, and are as diagnostic as characters that discriminate between *Choeroniscus* and *Hylonycteris*. Furthermore, the standard karyotypic data do not indicate a closer relationship between *Musonycteris* and *Choeronycteris* than between either and *Hylonycteris*.

We wish to thank Avelino B. Villa S., Direccion General de Fauna Silvestre, and Jorge E. Mendoza, Proyectos Tecnicos Faunisticos, México, for their kind assistance in obtaining collecting permits. Field work was supported by the Institute of Museum Research, Texas Tech University, and NSF Grant DEB-8D-04293 to R. J. Baker.

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ON THE BATS OF WESTERN MINAS GERAIS, BRASIL

BRYAN P. GLASS AND CHRISTIANE DA ENCARNAÇÃO

From February through May 1978, the authors surveyed the mammal fauna in the vicinity of Serra da Canastra National Park and São Roque de Minas in the state of Minas Gerais, Brasil. The areas studied lie about 250 km. W Belo Horizonte, the state capital, at approximately 21°S, 47°W. This paper reports on the bats collected during the survey period.

A search of the published literature revealed only one record of a bat from the region, a specimen of *Myotis nigricans* reported from Piumí, about 60 km. E São Roque, by LaVal (Sci. Bull., Los Angeles Co. Mus. Nat. Hist., 15:1-54, 1973). It therefore seems timely to record the occurrence of additional species from that area.

Serra da Canastra is a high, narrow plateau, with an east-west orientation, varying between 1033 and 1493 meters in elevation; the highest points are on the east end. On the north, east, and south, the plateau border consists of steep slopes and cliffs some 300 or more meters high. The Rio São Francisco, one of eastern Brasil's principal rivers, has its source on the southeastern part of the plateau, and leaves it via a narrow gorge and a 200-meter waterfall, the Casca d'Anta (See Fig. 1).

The village of São Roque lies about eight kilometers northeast of the eastern tip of the plateau and is approximately 400 meters lower in elevation. The terrain surrounding São Roque is hilly, dissected by streams in steep-sided valleys. The original vegetation seems to have been continuous forest. Although lower slopes of the hills have been cleared for pasture, and the less declivitous areas are planted to a great variety of crops, many of the hilltops still retain caps of dense forest. Road cuts in this populous area reveal a sandy topsoil of great depth, usually without any evident subsurface horizons. As one would expect, erosion is severe during the rainy season, and the streams carry a heavy silt burden.

By contrast, the plateau itself has a rocky core (principally of Precambrian rock), with much of the median ridge covered with a layer of lateritic iron nodules, either at or near the surface. This impervious crown capping the plateau resists water penetration, resulting in rapid runoff during the summer rainy season, which in turn produces steeply sloping stream banks. These streams end in falls or cataracts where they finally reach the border of the rocky uplift.

The vegetation of the plateau is principally grassland, and records of early exploration indicate that it was the same as early as 1814. Several individual ranches (fazendas) occupy the plateau, and grazing seems to have been continuous for at least 150 years. During that time, frequent burning in the dry season seems to have become a general practice, and in recent years has been so extensive that any part of the plateau could be expected to have been burned within the previous three to five years. As a result, even those upland areas with sufficient depth of soil to support tree growth are vegetated mostly with shrubs, and the few trees present are fire scarred. True forest, consisting of tall trees, palms, tree ferns, and vines, is limited to the vicinity of streams and is only a few meters wide, except in the few places where the confluence of two or more large streams converge. At those points, forest areas are often more extensive and encompass several hectares. Near the sources of small streams, the woody vegetation has become progressively reduced until nothing but shrubs remain. The branches of these shrubs interlock over the water to form a green tunnel.

The only parts of the plateau where there has been any cultivation is adjacent to the scattered ranch houses, where the occupants maintain small kitchen gardens and orchards. Brasilian orchards nearly always contain citrus trees of several varieties, and often have mangoes, cashews, and other tropical fruiting trees as well. Bananas are often planted adjacent to woody orchards, but are usually peripheral, and one often finds clumps of bananas where there are no other fruit-bearing plants. Spaces between clumps of bananas, as well as the areas below the branches of large trees and between rows of fruit trees, are excellent places to set mist nets.

Other good netting spots include places where trails cut through the shrubby cover along small streams. By contrast, no bats were taken in nets set in dry forest, along the forest edge adjacent to grassland, or in the vicinity of large rocky outcrops.

One small cave harboring a colony of vampires, *Desmodus rotundus*, was discovered. However, it is located on a cliff near the north park boundary (Fig. 1, site A) and is accessible only by rope; thus, mist netting was impractical. Furthermore, the narrow confines of the cave made hand-netting impossible. With the exception of these vampires, all bats discussed in this paper were taken in mist nets.

Collecting sites included seven localities within the park boundaries (see Fig. 1) and four in the vicinity of São Roque. The localities within the park are as follows: *Station 1,* Fazenda Chico Cera; two nets were set in the orchard on 29 March and one was set across the headwater stream of Corrego Mata Cavalo on 4 April. *Station 2,* Campsite beside riverine forest near headwaters of Corrego do Barbaro; one net was set along a path through the forest on 7 and 8 April. *Station 3,* Fazenda das Pedras at the junction of Corrego das Rolinhos and Corrego dos Cochos; one net was set beside the riverine forest and another was set between two clumps of banana plants on the evenings of 15, 16, and 8 April. *Station 4,* A fazenda called "weather station" about 5 km. W headwaters of Rio São Francisco, alongside a large brush-covered rockpile; two nets were set beside the rocks on 23 February. *Station 5,* Campsite above Casca d'Anta waterfall; one net was set on 10 and 13 May across the Corrego das Lavras. *Station 6,* Fazenda Casca d'Anta about 2 km. below waterfall; nets were set on 20, 21, and 23 May and at campsite one kilometer upstream from Fazenda Casca d'Anta (not marked separately from Station 6); two nets were set on 19 May, one across a road and one across a path entering the forest below the waterfall.

The four collecting sites outside the park do not appear on Fig. 1. They are: 1) In the yard of a home in São Roque; two nets were set on 3 March. 2) Fazenda Itamar about 5 km. S São Roque on the park road; two nets were set on 16 and 17 March. 3) Fazenda Rio do Peixe, 1 km. W São Roque; one net was set in a banana orchard 26 and 27 February, and one was set beside a cattle shed on 26 February and moved to a mango orchard on 27 February. 4) Fazenda Estiva about 6 km. NE São Roque; two nets were set in an orchard of mixed large fruit trees on 18 and 20 February.

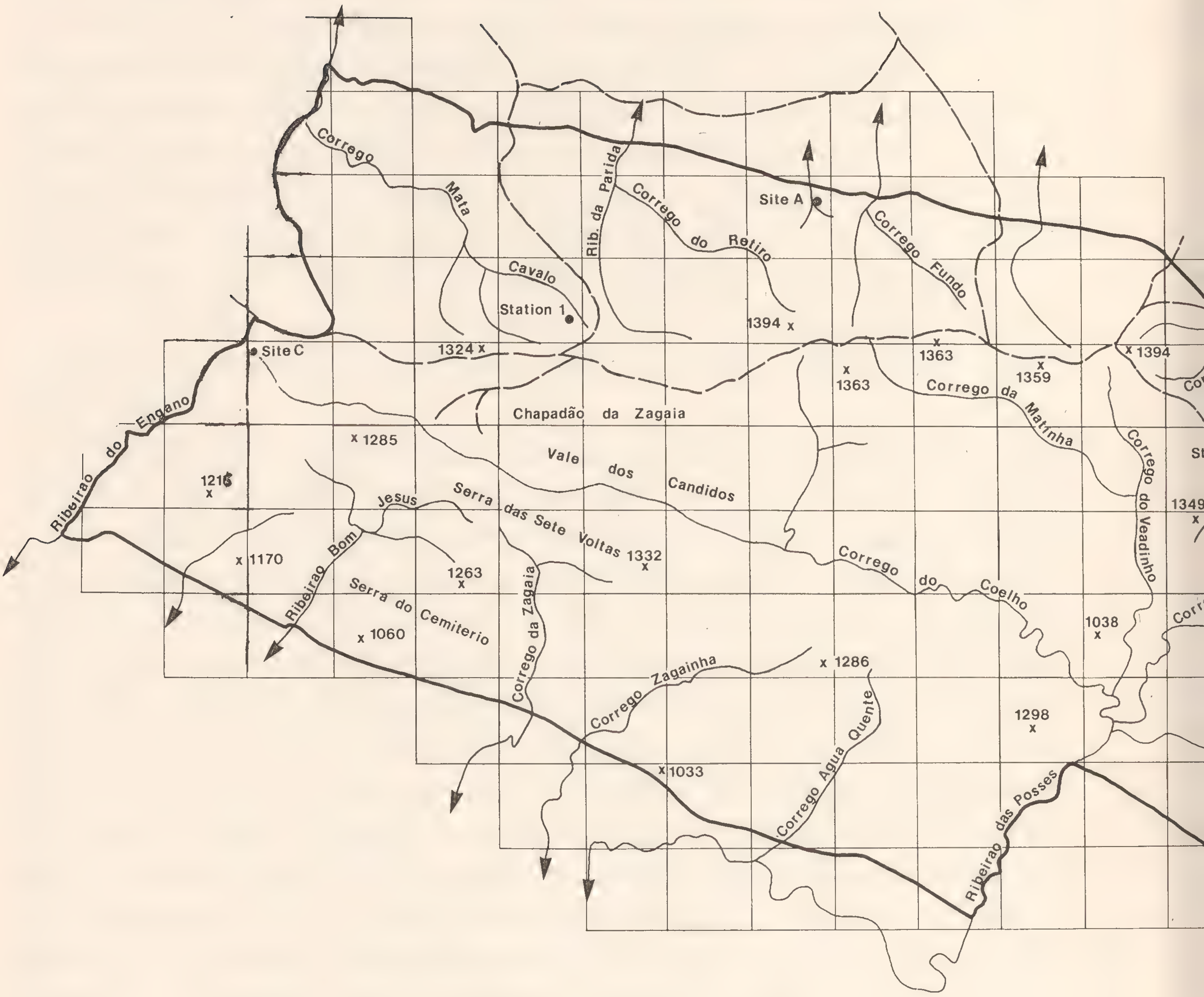
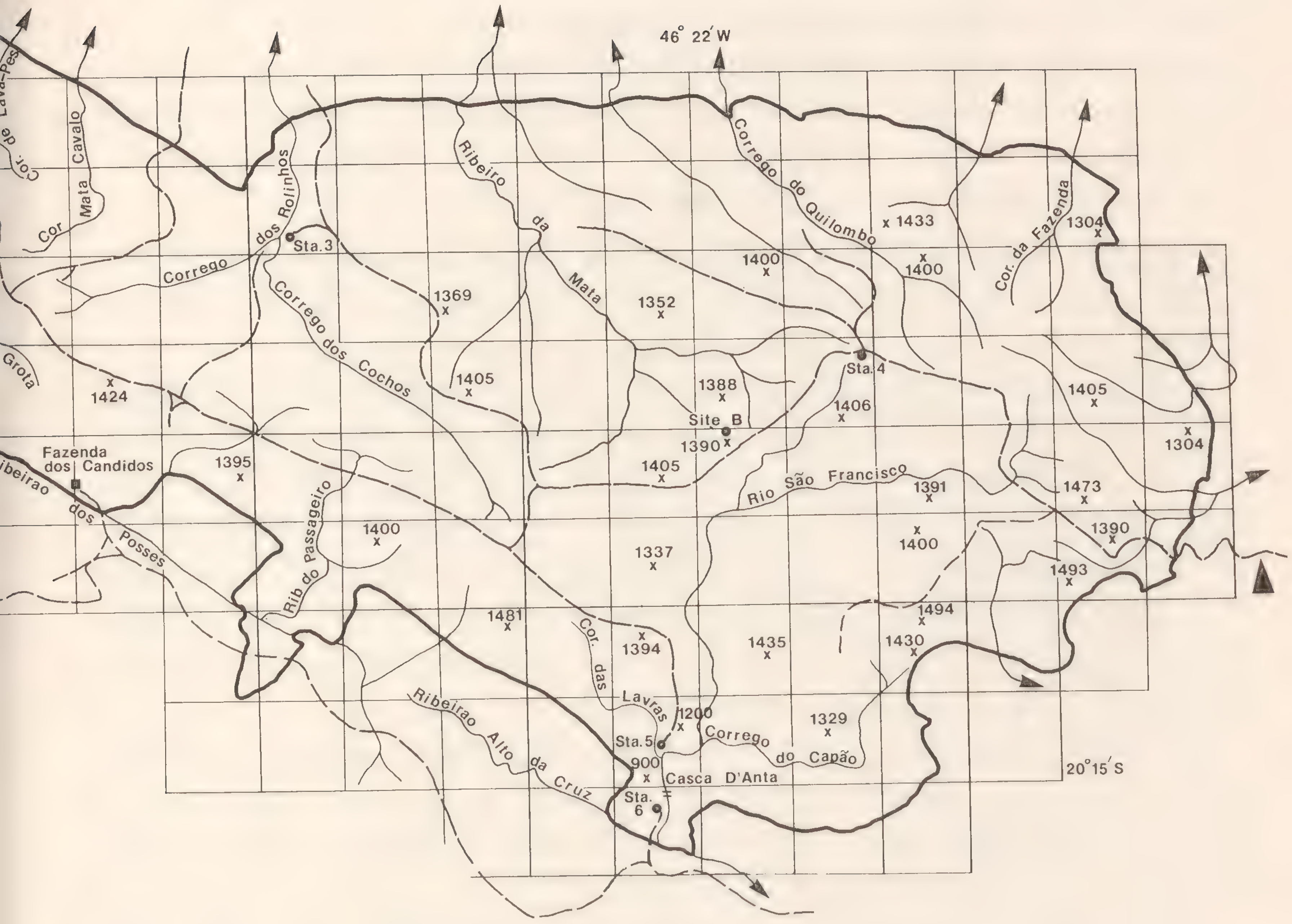


FIG. 1.—Map of Serra da Canastra National Park. Grid intervals are 2 km., dashed lines are negotiable roads, and collection stations are indicated by number. São Roque lies about eight kilometers (by air) northeast of the point where the road leaves the park boundary (large arrow). The stations and marked sites include all areas where collecting was done, not just those where bats were taken.


46° 22′ W
Cor. de Lava-Pés
Cor. Mata Cavalo
Corrego dos Rolinhos
Sta. 3
Ribeiro da Mata
Corrego do Quilombo
x 1433
1400 x
x 1400
Cor. da Fazenda
1304 x
Grota
x 1424
Corrego dos Cochos
1369 x
1352 x
1405 x
1388 x
Site B
1390 x
Sta. 4
1406 x
1405 x
x 1304
Fazenda dos Candidos
Ribeirão dos Posses
1395 x
Rib. do Passageiro
1405 x
Rio São Francisco
1391 x
1473 x
1400 x
1337 x
x 1400
1390 x
1493 x
1481 x
Cor. das Lavras
x 1394
1435 x
1494 x
1430 x
1200 x
Corrego do Capão
1329 x
Ribeirão Alto da Cruz
Sta. 5
900 x
Casca D'Anta
Sta. 6
20° 15′ S

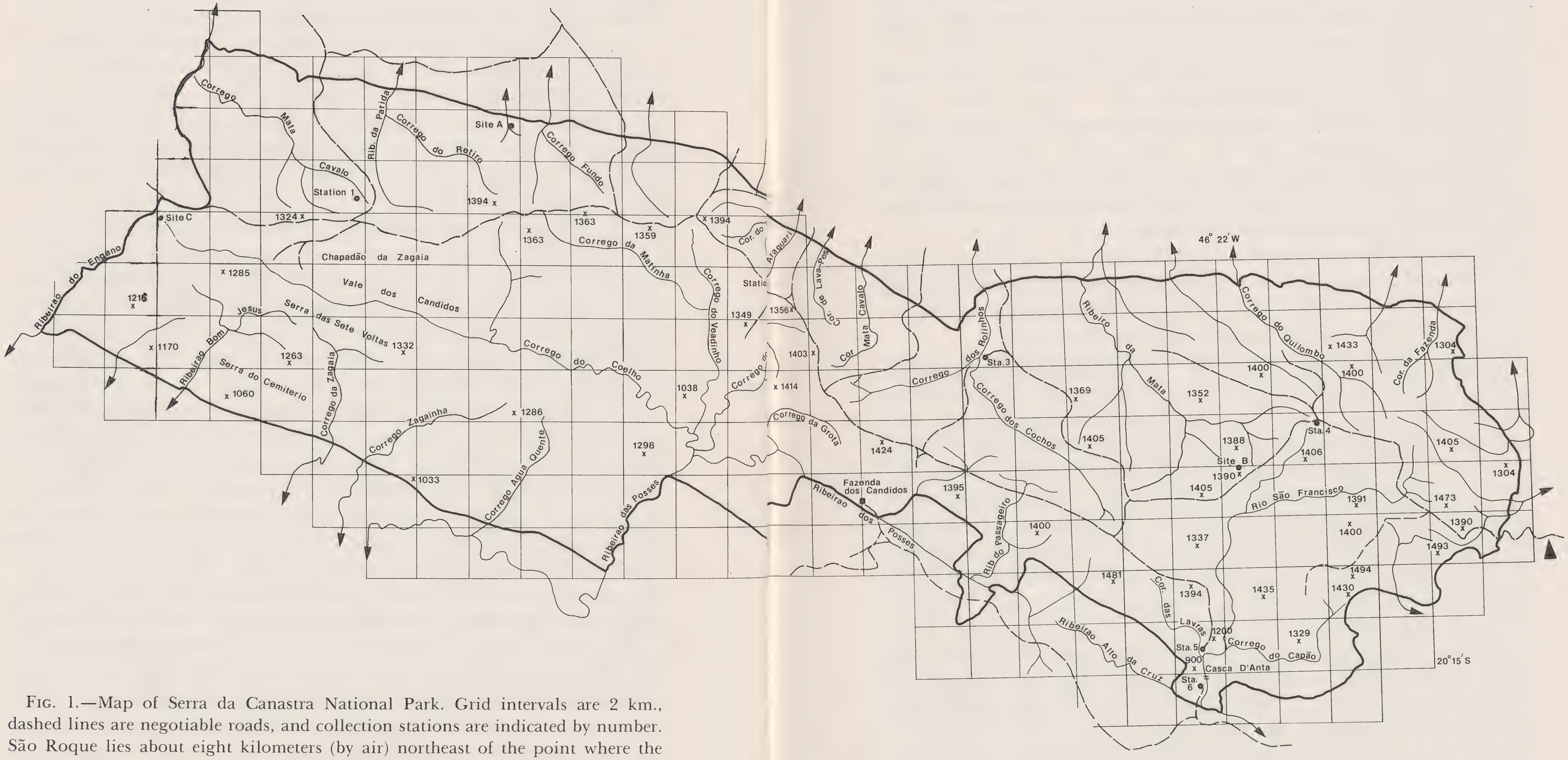


FIG. 1.—Map of Serra da Canastra National Park. Grid intervals are 2 km., dashed lines are negotiable roads, and collection stations are indicated by number. São Roque lies about eight kilometers (by air) northeast of the point where the road leaves the park boundary (large arrow). The stations and marked sites include all areas where collecting was done, not just those where bats were taken.

Family PHYLLOSTOMIDAE

Phyllostomus hastatus.—Four specimens were collected as follows: Station 1, Faz. Chico Cera orchard (1); Faz. Itamar (1); and Faz. Rio do Peixe (2). One male from Rio do Peixe had testes measuring 16 by 6 mm.

Micronycteris minuta.—A single specimen of this species was taken at Station 6 above Casca d'Anta.

Glossophaga soricina.—Four of these bats were taken, all at Faz. Estiva.

Anoura geoffroyi.—Eighteen bats of this species were collected at Station 1, Faz. Chico Cera over Corrego Mata Cavalo (2); São Roque (1); Faz. Itamar (6); and Faz. Estiva (9).

Anoura caudifer.—Fourteen individuals were obtained as follows: Station 6, Faz. Casca d'Anta (2), one male with testes 6 by 6 mm.; Station 3, Faz. das Pedras (1), male with testes 6 by 5 mm. and epididymides partly distended; and Faz. Estiva (11).

Carollia perspicillata.—Seven specimens were collected: Station 1, Faz. Chico Cera over Corrego Mata Cavalo (4); and Faz Estiva (3).

Sturnira lilium.—Thirty-eight of this common phyllostomid were netted at the following localities: Station 1, Faz. Chico Cera in the orchard and over Corrego Mata Cavalo (7), one male had testes 6 by 4 mm.; Station 3, Faz. das Pedras (3), two males were juveniles with swollen knuckles; Station 6, Faz. Casca d'Anta (9), two males had testes 2 by 3 and 5 by 4 mm., respectively; Faz. Itamar (5); Faz. Rio do Peixe (3), one a lactating female; and Faz. Estiva (11), one a lactating female.

Artibeus lituratus.—Four of these bats were collected: Faz. Itamar (1); Faz. Rio do Peixe (1); and Faz. Estiva (2). These specimens seem large for *A. lituratus,* one with a forearm of 73 mm. and the others measuring approximately 78.

Vampyrops lineatus.—Ten specimens were taken as follows: Station 1, Faz. Chico Cera orchard (1); Station 3, Faz. das Pedras (5); Station 6, Faz. Casca d'Anta orchard (1); and Faz. Rio do Peixe (3).

Desmodus rotundus.—Ten vampires were captured: Station 1, Faz. Chico Cera over Corrego Mata Cavalo (1); Station 6, Faz. Casca d'Anta orchard (4), one male with testes 9 by 8 mm., one with testes 8 by 7, and one female carrying a full-term fetus; and Faz. Rio do Peixe (5). As previously mentioned, about 25 of these bats were seen in the cave at Site A (Fig. 1). Horses with vampire bites were observed at Faz. Rio Peixe, Faz. Estiva, and at Faz. dos

Candidos, which lies inside the park boundary about 15 km. W Casca d'Anta.

Family Vespertilionidae

Myotis nigricans.—Three of these small bats were collected: one, which escaped from a holding cage, was netted over the Corrego Mata Cavalo at Faz. Chico Cera (Station 1); and two were taken from Station 5 above Casca d'Anta. A fourth specimen escaped from a net set beside a house in São Roque, the roof of which harbored a small colony of bats presumed to be this species. LaVal (*op. cit.*) indicated that *nigricans* is the only species of *Myotis* known to occur in western Minas Gerais.

Lasiurus ega.—Three specimens were netted, all from around banana plants at Station 3, Faz. das Pedras. One male had large testes and engorged epididymides.

Discussion

A total of 116 specimens of 12 species was collected during 37 net nights, for an average of 3.14 bats per net night. However, nets set at Station 6 (not in the orchard), at Stations 2 and 4, a total of six net nights, yielded no bats. Productive nets caught an average of 3.74 bats per night. All productive nets were set either in or near orchards, or were across streams bordered by bushes.

Of the species taken, five are frugivorous (*Phyllostomus hastatus, Carollia perspicillata, Artibeus lituratus, Vampyrops lineatus,* and *Sturnira lilium*) and three (*Glossophaga soricina, Anoura geoffroyi,* and *Anoura caudifer*) are nectarivorous; of these, *Sturnira lilium* and *Anoura geoffroyi* were the only ones captured both in orchards and over water. Vampires were netted over water, in orchards, and around banana plantings. Of the 12 species collected, eight occurred both on the plateau and at lower elevations; two (*Micronycteris minuta* and *Lasiurus ega*) were taken only on the plateau, and two (*Glossophaga soricina* and *Artibeus lituratus*) were netted at a lower elevations. Of interest is the observation that all vampire bites observed were on horses. The residents of this part of Brasil insist that no animals except horses are ever bitten by vampires; no cattle or swine with vampire bites were observed during this study.

Acknowledgments

Appreciation and thanks are extended to the late Dr. Ivens Pinto Franqueira, State Director of the Brasilian Institute of Forestry Development (IBDF) of the Ministry of Agriculture for his enthusiastic support of this study. Thanks also are expressed to the Administration of the Oklahoma State University for granting sabbatical leave to the senior author in order for him to participate in this project.

Specimens are on deposit in the collections of IBDF (Minas Gerais), Cx. Postal 1304, 30.000 Belo Horizonte, MG, Brasil.

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REVISED CHECKLIST OF NORTH AMERICAN MAMMALS NORTH OF MEXICO, 1982

J. Knox Jones, Jr., Dilford C. Carter, Hugh H. Genoways,
Robert S. Hoffmann, and Dale W. Rice

Faunal checklists provide a ready reference for many scientific endeavors, both in the laboratory and in the field, and are particularly useful to students. Since publication three years ago (Jones *et al.*, 1979) of a revised checklist of North American mammals, demand for the list has exceeded the supply set aside for general distribution and sale. Furthermore, the recent publication of *The mammals of North America* (Hall, 1981), more or less complete in terms of accounting for pertinent published literature through June of 1977, provided a convenient departure point for preparation of a new list.

We have attempted to include in this version of the checklist all species of Recent mammals (a few of which now may be extinct) in North America and adjacent waters occurring to the north of Mexico as recognized in the published literature through March of 1982. Significant departures from Hall's (1981) treatment are discussed beyond and are primarily of three different kinds: 1) differences in opinion regarding certain contemporary systematic works; 2) Hall's aversion to rulings of the International Commission on Zoological Nomenclature; and 3), of course, published studies postdating the completion of his text. Our list represents a concensus among the five authors but does not necessarily imply complete agreement on all controversial points.

As most readers are aware, various species of mammals not native to North America have been introduced here over the years.

Nine such taxa (identified by an asterisk) are included in the checklist because they currently occur in the wild state in numbers sufficient to justify listing them. Other species, such as the blackbuck (*Antilope cervicapra*), axis deer (*Cervus axis*), sika deer (*Cervus nippon*), ibex (*Capra ibex*), and oryx (*Oryx gazella*), now occur outside confinement and some of these likely will have to be included in subsequent checklists.

Nomenclatorial Departures from Hall (1981) and Other Notes

We have documented below those instances in which usage in this checklist differs significantly from that of Hall (1981) and have referred to the authoritative source(s) in most cases. A few of the same changes also are cited in the addenda to Hall's compendium (pages 1177-1181). Some other pertinent comments that may explain the current list of recognized species of mammals occurring in North America (north of Mexico) are included.

Marsupials

Some recent authors have accorded the Marsupialia superordinal rank and placed the Didelphidae in one or another of several orders contained in such a grouping. Because there is as yet no clear consensus in the literature as to the probable correct classification, we adopt the conservative course of continuing to recognize Marsupialia at the ordinal level, as did Hall.

Insectivores

The following information relates to members of the genus *Sorex*: *S. jacksoni* is listed as a distinct species following Junge and Hoffmann (1981); *S. trigonirostris* is a synonym of *S. vagrans* according to Hennings and Hoffmann (1977) and *S. sinuosus* was regarded as a subspecies of *S. ornatus* by Junge and Hoffmann (1981); *S. monticolus* and *S. pacificus* are listed as species distinct from *S. vagrans* (Hennings and Hoffmann, 1977; Junge and Hoffmann, 1981); *S. tundrensis* is considered a specific-level taxon following Youngman (1975) and subsequent authors; *S. arizonae* was described as new by Diersing and Hoffmeister (1977); and *Microsorex* (*S. hoyi*) was reduced from generic to subgeneric rank by Diersing (1980).

Evidence is accumulating that the races *haydeni* (van Zyll de Jong, 1980; Junge and Hoffmann, 1981) and *fontinalis* (Kirkland, 1977; Junge and Hoffmann, 1981) may be distinct at the specific level from *S. cinereus*, but additional data are needed to clarify the status of these populations. Furthermore, *S. alaskanus*, admitted here, may be a synonym of *S. palustris* (Hall, 1981; Junge and Hoffmann, 1981).

In the genus *Blarina*, we recognize *carolinensis* as separate from *brevicauda* on the basis of several recent studies, and we also recognize the species *B. hylophaga* following George *et al.* (1981). *B. telmalestes* was reduced to subspecific rank under *brevicauda* by Handley (1979).

Bats

Following Smith (1972), we recognize the family Mormoopidae (as opposed to referring these bats to the subfamily Chilonycterinae of the family Phyllostomidae) and, following Opinion 462 of the International Commission on Zoological Nomenclature, employ *Mormoops* rather than *Aello* for ghost-faced bats. *Macrotus californicus* seems to be the correct name for the leaf-nosed bat inhabiting the southwestern United States (Davis and Baker, 1974; Greenbaum and Baker, 1976), and *Leptonycteris sanborni* is retained as the correct name for the species listed by Hall as *L. yerbabuenae* (see Watkins *et al.*, 1972). Handley (1980) has explained why Phyllostomidae, not Phyllostomatidae, is the proper spelling of this family-group name.

The specific epithet *Myotis leibii* is used in preference to *M. subulatus* following Glass and Baker (1965) and subsequent authors. On the basis of Opinion 111 of the International Commission, the generic name *Lasiurus* is adopted (rather than *Nycteris*) for all lasiurine bats, and, following Williams *et al.* (1970), *Idionycteris* is recognized as a genus distinct from *Plecotus*.

Although it was not adopted here, van Zyll de Jong (1979) has made the suggestion that the subspecies *Myotis keenii keenii* and *M. k. septentrionalis* are distinct at the specific level, and further work might substantiate this contention, and Freeman (1981) employed the generic name *Nyctinomops* for *Tadarida femorosacca* and *T. macrotis*.

Rodents

Sciuridae.—We follow Nadler *et al.* (1977), supported by additional as yet unpublished evidence, in recognizing *Tamias* as the single generic name for all chipmunks (but see Ellis and Maxon, 1979). Additionally, *Spermophilus elegans* is recognized as distinct from *S. richardsonii* (Koeppl and Hoffmann, 1981), *Marmota broweri* is regarded as a species separate from *M. caligata* (Hoffmann *et al.*, 1979), and *Sciurus kaibabensis* was reduced to subspecific status under *S. aberti* by Hoffmeister and Diersing (1978).

Geomyidae.—The following remarks apply to the genus *Thomomys*: *T. bottae* is regarded as distinct from *T. umbrinus* on the basis of Hoffmeister's (1969) findings and numerous subsequent publications; Thaeler (1968) is followed in listing *T. townsendii* as distinct from *T. umbrinus;* and the species *idahoensis* and *clusius* were recognized by Thaeler (1972) and Thaeler and Hinesley (1979), respectively.

In *Geomys,* we follow Tucker and Schmidly (1981) in arranging *G. attwateri* as distinct from *G. bursarius,* and Williams and Genoways (1980) in regarding the nominal species *colonus, fontanelus,* and *cumberlandius* as junior synonyms of *G. pinetis,* with *fontanelus* as the only one recognized at the subspecific level.

Heteromyidae.—In this group, we follow Schmidly and Hendricks (1976) and Baumgardner and Schmidly (1981) in listing *Dipodomys compactus* as a separate species and Patton *et al.* (1976) in recognizing *D. californicus* as distinct from *D. heermanni.*

Cricetidae.—In the list of cricetines, we have included *Oryzomys couesi* (Benson and Gehlbach, 1979) and *O. argentatus,* recently described by Spitzer and Lazell (1978). *Peromyscus melanotis* also has been added because Bowers (1974) recorded populations from Arizona, and the generic name of the Florida mouse is changed to *Podomys* following Carleton (1980). *Peromyscus comanche* was recognized as a distinct species by Johnson and Packard (1974), a work seemingly overlooked by some subsequent workers.

Onychomys arenicola was shown to be a distinctive third species in that genus by Hinesley (1979), and *Neotoma devia* was recognized as separate from *N. lepida* by Mascarello (1978).

Among the microtines, *Arborimus* is recognized as distinct at the generic level (Johnson, 1973). We have not followed some recent authors (Martin, 1974, and Chaline and Mein, 1979, for example) in regarding *Pitymys* (including *Microtus ochrogaster* and *M. pinetorum*) as separable at the generic level from *Microtus* or in recognizing *Pitymys* as distinct in a more restrictive sense (van der Meulen, 1978), nor have we followed others (Hooper and Hart, 1962, and Jannett and Jannett, 1974, for example) in recognizing *Arvicola* as a separate genus; both these matters are deserving of further analysis.

We have followed Hall in listing only three species of *Dicrostonyx.* The systematics of this genus are complex and not yet fully understood, and some sources (Rausch, 1977, for example) have recognized more than three species in North America. Finally, we retain the familial name Cricetidae, in preference to including all these mice and rats in Muridae, although this matter has not been resolved finally in the literature.

Carnivores

Hall submerged *Vulpes macrotis* under *V. velox* because of alleged hybridization at some places where the two meet geographically, but we regard them as distinct species (see Rohwer and Kilgore, 1973; Thornton and Creel, 1975; Waithman and Roest, 1977). Van Gelder (1978) listed all canids treated here as species of the genus *Canis,* but this arrangement has not as yet gained wide acceptance. In the Ursidae, we recognize a single species of grizzly or brown bear, *Ursus arctos,* as opposed to the lengthy list of taxa included by Hall.

The pinnipeds represent a biphyletic assemblage of arctoid carnivores (Tedford, 1976) and are here listed as families (three) of the Carnivora, the Odobenidae recognized following Repenning and Tedford (1977). *Arctocephalus townsendi* is a species separate from *A. philippii* according to Repenning *et al.* (1971). We follow Opinion 467 of the International Commission on Zoological Nomenclature in listing *Odobenus* as the correct generic name for the walrus.

In the Mustelidae, we follow Kurtén and Rausch (1959) and most recent authors in regarding the wolverines of the Holarctic as a single species, *Gulo gulo.* Furthermore, Mead (1968) has demonstrated that *Spilogale putorius* and *S. gracilis* are geographically and reproductively isolated and deserving of recognition as separate species. In the family Phocidae, Shaughnessy and Fay (1977) have shown that *Phoca largha* represents a distinct species, and Burns and Fay (1970) regarded *Histriophoca, Pusa,* and *Pagophilus* as subgenera of *Phoca* (Hall recognized them as genera).

We tentatively use the generic name *Felis* for all North American felids. There is, however, some evidence for use of *Panthera,* at least for *F. onca,* and there is still disagreement in the literature as to whether *Lynx* should be accorded generic rank and whether in that group *canadensis* should be regarded as a species distinct from the Old World *lynx* (see especially Werdelin, 1981).

Whales

The two great groups of living whales are here listed as separate orders in accord with much of the recent cetological literature. The following comments apply to taxa recorded in the checklist: *Eschrichtius robustus* is given as the appropriate name for the gray whale (see Rice and Wolman, 1971); the specific name *nesarnack* is not employed in *Tursiops* following Hershkovitz (1966) and Rice (1977), and *T. gillii* is regarded as a synonym of *T. truncatus* (Mitchell, 1975); *Stenella frontalis* and *S. attenuata* both are included, but well may prove to be conspecific; the specific name *Stenella plagiodon* is used in preference to *S. pernettensis* in accord with Opinion 1067 of the International Commission on Zoological Nomenclature; *Stenella clymene* is recognized following Perrin *et al.* (1981); *macrorhynchus* is employed as the specific name for the short-finned pilot whale because that name was selected in preference to *sieboldii* by the first reviser (Gray, 1871); the family Phocoenidae is separated from the Delphinidae as suggested by Barnes (1978); *Mesoplodon* is regarded as the correct generic name for beaked whales (Hershkovitz, 1966; Rice and Kinman, 1980); *Mesoplodon hectori* is included because this whale recently has been recorded from California (Mead, 1981); and *macrocephalus* is listed as the correct specific name for the sperm whale following Husson and Holthuis (1974).

Artiodactyls

In the Artiodactyla, we return to the use of the generic name *Tayassu* for the collared peccary following Wetzel (1977), and *Odocoileus* is used in place of *Dama* for the American deer as a result of Opinion 581 of the International Commission on Zoological Nomenclature. The antilocaprids have been retained as a separate family, although O'Gara and Matson (1975) presented evidence suggesting that they should be considered a subfamily of Bovidae. See also Van Gelder (1977) on hybridization among artiodactyls.

ORDER MARSUPIALIA—Marsupials

FAMILY DIDELPHIDAE—New World Opossums

Didelphis virginiana .... Virginia Opossum

ORDER INSECTIVORA—Insectivores

FAMILY SORICIDAE—Shrews

Sorex cinereus	Cinereus or Masked Shrew
Sorex hydrodromus	Pribilof Island Shrew
Sorex jacksoni	St. Lawrence Island Shrew
Sorex lyelli	Mt. Lyell Shrew
Sorex preblei	Preble's Shrew
Sorex longirostris	Southeastern Shrew
Sorex vagrans	Vagrant Shrew
Sorex monticolus	Dusky or Montane Shrew
Sorex pacificus	Pacific Shrew
Sorex ornatus	Ornate Shrew
Sorex tenellus	Inyo Shrew
Sorex nanus	Dwarf Shrew
Sorex palustris	Water Shrew
Sorex alaskanus	Glacier Bay Water Shrew
Sorex bendirii	Pacific Water or Marsh Shrew
Sorex fumeus	Smoky Shrew
Sorex dispar	Long-tailed or Rock Shrew
Sorex gaspensis	Gaspé Shrew
Sorex arcticus	Arctic Shrew
Sorex tundrensis	Tundra Shrew
Sorex trowbridgii	Trowbridge's Shrew
Sorex merriami	Merriam's Shrew
Sorex arizonae	Arizona Shrew
Sorex hoyi	Pygmy Shrew
Blarina brevicauda	Northern Short-tailed Shrew
Blarina carolinensis	Southern Short-tailed Shrew
Blarina hylophaga	Elliot's Short-tailed Shrew
Cryptotis parva	Least Shrew
Notiosorex crawfordi	Desert Shrew

FAMILY TALPIDAE—Moles

Neurotrichus gibbsii	Shrew-mole
Scapanus townsendii	Townsend's Mole
Scapanus orarius	Coast Mole
Scapanus latimanus	Broad-footed Mole
Parascalops breweri	Hairy-tailed Mole
Scalopus aquaticus	Eastern Mole
Condylura cristata	Star-nosed Mole

ORDER CHIROPTERA—Bats

FAMILY MORMOOPIDAE—Mormoopid Bats

Mormoops megalophylla	Ghost-faced Bat

FAMILY PHYLLOSTOMIDAE—Phyllostomid Bats

Macrotus californicus	California Leaf-nosed Bat
Choeronycteris mexicana	Long-tongued Bat
Leptonycteris nivalis	Mexican Long-nosed Bat
Leptonycteris sanborni	Sanborn's Long-nosed Bat
Diphylla ecaudata	Hairy-legged Vampire

FAMILY VESPERTILIONIDAE—Vespertilionid Bats

Myotis lucifugus	Little Brown Myotis
Myotis yumanensis	Yuma Myotis
Myotis austroriparius	Southeastern Myotis
Myotis grisescens	Gray Myotis
Myotis velifer	Cave Myotis
Myotis keenii	Keen's Myotis
Myotis evotis	Long-eared Myotis
Myotis auriculus	Southwestern Myotis
Myotis thysanodes	Fringed Myotis
Myotis sodalis	Indiana or Social Myotis
Myotis volans	Long-legged Myotis
Myotis californicus	California Myotis
Myotis leibii	Small-footed Myotis
Lasionycteris noctivagans	Silver-haired Bat
Pipistrellus hesperus	Western Pipistrelle
Pipistrellus subflavus	Eastern Pipistrelle
Eptesicus fuscus	Big Brown Bat
Lasiurus borealis	Red Bat
Lasiurus seminolus	Seminole Bat
Lasiurus cinereus	Hoary Bat
Lasiurus intermedius	Northern Yellow Bat
Lasiurus ega	Southern Yellow Bat
Nycticeius humeralis	Evening Bat
Euderma maculatum	Spotted Bat
Plecotus townsendii	Townsend's Big-eared Bat
Plecotus rafinesquii	Rafinesque's Big-eared Bat
Idionycteris phyllotis	Allen's Big-eared Bat
Antrozous pallidus	Pallid Bat

FAMILY MOLOSSIDAE—Molossid Bats

Tadarida brasiliensis	Brazilian Free-tailed Bat
Tadarida femorosacca	Pocketed Free-tailed Bat

Tadarida macrotis	Big Free-tailed Bat
Eumops perotis	Western Mastiff Bat
Eumops underwoodi	Underwood's Mastiff Bat
Eumops glaucinus	Wagner's Mastiff Bat

ORDER EDENTATA—Edentates

FAMILY DASYPODIDAE—Armadillos

Dasypus novemcinctus	Nine-banded Armadillo

ORDER LAGOMORPHA—Lagomorphs

FAMILY OCHOTONIDAE—Pikas

Ochotona collaris	Collared Pika
Ochotona princeps	Pika

FAMILY LEPORIDAE—Hares and Rabbits

Sylvilagus idahoensis	Pygmy Rabbit
Sylvilagus bachmani	Brush Rabbit
Sylvilagus palustris	Marsh Rabbit
Sylvilagus floridanus	Eastern Cottontail
Sylvilagus transitionalis	New England Cottontail
Sylvilagus nuttallii	Nuttall's Cottontail
Sylvilagus audubonii	Desert Cottontail
Sylvilagus aquaticus	Swamp Rabbit
*Oryctolagus cuniculus**	European Rabbit
Lepus americanus	Snowshoe Hare
Lepus othus	Alaska Hare
Lepus arcticus	Arctic Hare
Lepus townsendii	White-tailed Jack Rabbit
Lepus californicus	Black-tailed Jack Rabbit
Lepus callotis	White-sided Jack Rabbit
Lepus alleni	Antelope Jack Rabbit
*Lepus capensis**	Cape or European Hare

ORDER RODENTIA—Rodents

FAMILY APLODONTIIDAE—Mountain Beaver

Aplodontia rufa	Mountain Beaver

FAMILY SCIURIDAE—Squirrels

Tamias striatus	Eastern Chipmunk
Tamias alpinus	Alpine Chipmunk
Tamias minimus	Least Chipmunk
Tamias amoenus	Yellow-pine Chipmunk
Tamias townsendii	Townsend's Chipmunk

Tamias ochrogenys	Yellow-cheeked Chipmunk
Tamias senex	Allen's Chipmunk
Tamias siskiyou	Siskiyou Chipmunk
Tamias sonomae	Sonoma Chipmunk
Tamias merriami	Merriam's Chipmunk
Tamias obscurus	California Chipmunk
Tamias dorsalis	Cliff Chipmunk
Tamias quadrivittatus	Colorado Chipmunk
Tamias ruficaudus	Red-tailed Chipmunk
Tamias cinereicollis	Gray-collared Chipmunk
Tamias canipes	Gray-footed Chipmunk
Tamias quadrimaculatus	Long-eared Chipmunk
Tamias speciosus	Lodgepole Chipmunk
Tamias panamintinus	Panamint Chipmunk
Tamias umbrinus	Uinta Chipmunk
Tamias palmeri	Palmer's Chipmunk
Marmota monax	Woodchuck
Marmota flaviventris	Yellow-bellied Marmot
Marmota broweri	Alaska Marmot
Marmota caligata	Hoary Marmot
Marmota olympus	Olympic Marmot
Marmota vancouverensis	Vancouver Marmot
Ammospermophilus harrisii	Harris' Antelope Squirrel
Ammospermophilus leucurus	White-tailed Antelope Squirrel
Ammospermophilus interpres	Texas Antelope Squirrel
Ammospermophilus nelsoni	Nelson's Antelope Squirrel
Spermophilus townsendii	Townsend's Ground Squirrel
Spermophilus washingtoni	Washington Ground Squirrel
Spermophilus brunneus	Idaho Ground Squirrel
Spermophilus richardsonii	Richardson's Ground Squirrel
Spermophilus elegans	Wyoming Ground Squirrel
Spermophilus armatus	Uinta Ground Squirrel
Spermophilus beldingi	Belding's Ground Squirrel
Spermophilus columbianus	Columbian Ground Squirrel
Spermophilus parryii	Arctic Ground Squirrel

Spermophilus tridecemlineatus	Thirteen-lined Ground Squirrel
Spermophilus mexicanus	Mexican Ground Squirrel
Spermophilus spilosoma	Spotted Ground Squirrel
Spermophilus franklinii	Franklin's Ground Squirrel
Spermophilus variegatus	Rock Squirrel
Spermophilus beecheyi	California Ground Squirrel
Spermophilus mohavensis	Mohave Ground Squirrel
Spermophilus tereticaudus	Round-tailed Ground Squirrel
Spermophilus lateralis	Golden-mantled Ground Squirrel
Spermophilus saturatus	Cascade Golden-mantled Ground Squirrel
Cynomys ludovicianus	Black-tailed Prairie Dog
Cynomys leucurus	White-tailed Prairie Dog
Cynomys parvidens	Utah Prairie Dog
Cynomys gunnisoni	Gunnison's Prairie Dog
Sciurus carolinensis	Gray Squirrel
Sciurus niger	Fox Squirrel
Sciurus nayaritensis	Nayarit Squirrel
Sciurus arizonensis	Arizona Gray Squirrel
Sciurus griseus	Western Gray Squirrel
Sciurus aberti	Abert's Squirrel
Tamiasciurus hudsonicus	Red Squirrel
Tamiasciurus douglasii	Douglas' Squirrel
Glaucomys volans	Southern Flying Squirrel
Glaucomys sabrinus	Northern Flying Squirrel

FAMILY GEOMYIDAE—Pocket Gophers

Thomomys umbrinus	Southern Pocket Gopher
Thomomys bottae	Botta's Pocket Gopher
Thomomys townsendii	Townsend's Pocket Gopher
Thomomys talpoides	Northern Pocket Gopher
Thomomys clusius	Wyoming Pocket Gopher
Thomomys idahoensis	Idaho Pocket Gopher
Thomomys mazama	Western Pocket Gopher
Thomomys monticola	Mountain Pocket Gopher
Thomomys bulbivorus	Camas Pocket Gopher
Geomys bursarius	Plains Pocket Gopher
Geomys attwateri	Attwater's Pocket Gopher
Geomys arenarius	Desert Pocket Gopher
Geomys personatus	Texas Pocket Gopher
Geomys pinetis	Southeastern Pocket Gopher
Pappogeomys castanops	Yellow-faced Pocket Gopher

FAMILY HETEROMYIDAE—Heteromyids

Perognathus fasciatus	Olive-backed Pocket Mouse
Perognathus flavescens	Plains Pocket Mouse
Perognathus flavus	Silky Pocket Mouse
Perognathus longimembris	Little Pocket Mouse
Perognathus amplus	Arizona Pocket Mouse
Perognathus inornatus	San Joaquin Pocket Mouse
Perognathus parvus	Great Basin Pocket Mouse
Perognathus alticola	White-eared Pocket Mouse
Perognathus xanthonotus	Yellow-eared Pocket Mouse
Perognathus formosus	Long-tailed Pocket Mouse
Perognathus baileyi	Bailey's Pocket Mouse
Perognathus hispidus	Hispid Pocket Mouse
Perognathus penicillatus	Desert Pocket Mouse
Perognathus intermedius	Rock Pocket Mouse
Perognathus nelsoni	Nelson's Pocket Mouse
Perognathus fallax	San Diego Pocket Mouse
Perognathus californicus	California Pocket Mouse
Perognathus spinatus	Spiny Pocket Mouse
Microdipodops megacephalus	Dark Kangaroo Mouse
Microdipodops pallidus	Pale Kangaroo Mouse
Dipodomys ordii	Ord's Kangaroo Rat
Dipodomys compactus	Gulf Coast Kangaroo Rat
Dipodomys microps	Chisel-toothed Kangaroo Rat
Dipodomys elephantinus	Big-eared Kangaroo Rat
Dipodomys venustus	Narrow-faced Kangaroo Rat
Dipodomys agilis	Agile Kangaroo Rat
Dipodomys heermanni	Heermann's Kangaroo Rat
Dipodomys californicus	California Kangaroo Rat
Dipodomys ingens	Giant Kangaroo Rat
Dipodomys panamintinus	Panamint Kangaroo Rat
Dipodomys stephensi	Stephens' Kangaroo Rat
Dipodomys spectabilis	Banner-tailed Kangaroo Rat
Dipodomys elator	Texas Kangaroo Rat
Dipodomys merriami	Merriam's Kangaroo Rat
Dipodomys nitratoides	Fresno Kangaroo Rat
Dipodomys deserti	Desert Kangaroo Rat
Liomys irroratus	Mexican Spiny Pocket Mouse

FAMILY CASTORIDAE—Beavers

Castor canadensis	Beaver

FAMILY CRICETIDAE—Cricetids

Oryzomys palustris	Marsh Rice Rat
Oryzomys couesi	Coues' Rice Rat
Oryzomys argentatus	Key Rice Rat
Reithrodontomys montanus	Plains Harvest Mouse
Reithrodontomys humulis	Eastern Harvest Mouse
Reithrodontomys megalotis	Western Harvest Mouse
Reithrodontomys raviventris	Salt-marsh Harvest Mouse
Reithrodontomys fulvescens	Fulvous Harvest Mouse
Peromyscus eremicus	Cactus Mouse
Peromyscus merriami	Merriam's Mouse
Peromyscus californicus	California Mouse
Peromyscus polionotus	Oldfield Mouse
Peromyscus maniculatus	Deer Mouse
Peromyscus sitkensis	Sitka Mouse
Peromyscus melanotis	Black-eared Mouse
Peromyscus leucopus	White-footed Mouse
Peromyscus gossypinus	Cotton Mouse
Peromyscus crinitus	Canyon Mouse
Peromyscus boylii	Brush Mouse
Peromyscus attwateri	Texas Mouse
Peromyscus pectoralis	White-ankled Mouse
Peromyscus truei	Piñon Mouse
Peromyscus comanche	Palo Duro Mouse
Peromyscus difficilis	Rock Mouse
Podomys floridanus	Florida Mouse
Ochrotomys nuttalli	Golden Mouse
Baiomys taylori	Northern Pygmy Mouse
Onchomys leucogaster	Northern Grasshopper Mouse
Onchomys torridus	Southern Grasshopper Mouse
Onchomys arenicola	Mearns' Grasshopper Mouse
Sigmodon hispidus	Hispid Cotton Rat
Sigmodon arizonae	Arizona Cotton Rat
Sigmodon fulviventer	Tawny-bellied Cotton Rat
Sigmodon ochrognathus	Yellow-nosed Cotton Rat
Neotoma floridana	Eastern Woodrat
Neotoma micropus	Southern Plains Woodrat
Neotoma albigula	White-throated Woodrat

Neotoma lepida	Desert Woodrat
Neotoma devia	Arizona Woodrat
Neotoma stephensi	Stephens' Woodrat
Neotoma mexicana	Mexican Woodrat
Neotoma fuscipes	Dusky-footed Woodrat
Neotoma cinerea	Bushy-tailed Woodrat
Clethrionomys rutilus	Northern Red-backed Vole
Clethrionomys gapperi	Southern Red-backed Vole
Clethrionomys californicus	Western Red-backed Vole
Phenacomys intermedius	Heather Vole
Arborimus albipes	White-footed Vole
Arborimus longicaudus	Red Tree Vole
Microtus pennsylvanicus	Meadow Vole
Microtus breweri	Beach Vole
Microtus nesophilus	Gull Island Vole
Microtus montanus	Montane Vole
Microtus canicaudus	Gray-tailed Vole
Microtus californicus	California Vole
Microtus townsendii	Townsend's Vole
Microtus oeconomus	Tundra Vole
Microtus longicaudus	Long-tailed Vole
Microtus coronarius	Coronation Island Vole
Microtus mexicanus	Mexican Vole
Microtus chrotorrhinus	Rock Vole
Microtus xanthognathus	Yellow-cheeked or Taiga Vole
Microtus oregoni	Creeping Vole
Microtus miurus	Singing Vole
Microtus abbreviatus	St. Matthew Island Vole
Microtus ochrogaster	Prairie Vole
Microtus pinetorum	Woodland Vole
Microtus richardsoni	Water Vole
Lagurus curtatus	Sagebrush Vole
Neofiber alleni	Round-tailed Muskrat
Ondatra zibethicus	Muskrat
Lemmus sibiricus	Brown Lemming
Synaptomys cooperi	Southern Bog Lemming
Synaptomys borealis	Northern Bog Lemming
Dicrostonyx groenlandicus	Collared Lemming
Dicrostonyx exsul	St. Lawrence Island Collared Lemming
Dicrostonyx hudsonius	Labrador Collared Lemming

FAMILY MURIDAE—Murids

_Rattus rattus_*	Black Rat
_Rattus norvegicus_*	Norway Rat
_Mus musculus_*	House Mouse

FAMILY ZAPODIDAE—Jumping Mice

Zapus hudsonius	Meadow Jumping Mouse
Zapus princeps	Western Jumping Mouse
Zapus trinotatus	Pacific Jumping Mouse
Napaeozapus insignis	Woodland Jumping Mouse

FAMILY ERETHIZONTIDAE—New World Porcupines

Erethizon dorsatum	Porcupine

FAMILY MYOCASTORIDAE—Myocastorids

_Myocastor coypus_*	Nutria

ORDER CARNIVORA—Carnivores

FAMILY CANIDAE—Canids

Canis latrans	Coyote
Canis rufus	Red Wolf
Canis lupus	Gray Wolf
Alopex lagopus	Arctic Fox
Vulpes vulpes	Red Fox
Vulpes macrotis	Kit Fox
Vulpes velox	Swift Fox
Urocyon cinereoargenteus	Gray Fox
Urocyon littoralis	Channel Islands Gray Fox

FAMILY URSIDAE—Bears

Ursus americanus	Black Bear
Ursus arctos	Grizzly or Brown Bear
Ursus maritimus	Polar Bear

FAMILY OTARIIDAE—Eared Seals

Callorhinus ursinus	Northern Fur Seal
Arctocephalus townsendi	Guadalupe Fur Seal
Eumetopias jubatus	Northern Sea Lion
Zalophus californianus	California Sea Lion

FAMILY ODOBENIDAE—Walrus

Odobenus rosmarus	Walrus

FAMILY PROCYONIDAE—Procyonids

Bassariscus astutus	Ringtail
Procyon lotor	Raccoon
Nasua nasua	Coati

FAMILY MUSTELIDAE—Mustelids

Martes americana	Marten
Martes pennanti	Fisher
Mustela erminea	Ermine
Mustela nivalis	Least Weasel
Mustela frenata	Long-tailed Weasel
Mustela nigripes	Black-footed Ferret
Mustela vison	Mink
Gulo gulo	Wolverine
Taxidea taxus	Badger
Spilogale putorius	Eastern Spotted Skunk
Spilogale gracilis	Western Spotted Skunk
Mephitis mephitis	Striped Skunk
Mephitis macroura	Hooded Skunk
Conepatus mesoleucus	Hog-nosed Skunk
Conepatus leuconotus	Eastern Hog-nosed Skunk
Lutra canadensis	River Otter
Enhydra lutris	Sea Otter

FAMILY PHOCIDAE—Hair Seals

Phoca vitulina	Harbor Seal
Phoca largha	Spotted Seal
Phoca fasciata	Ribbon Seal
Phoca hispida	Ringed Seal
Phoca groenlandica	Harp Seal
Halichoerus grypus	Gray Seal
Erignathus barbatus	Bearded Seal
Cystophora cristata	Hooded Seal
Monachus tropicalis	West Indian Monk Seal
Mirounga angustirostris	Northern Elephant Seal

FAMILY FELIDAE—Cats

Felis onca	Jaguar
Felis concolor	Mountain Lion
Felis pardalis	Ocelot
Felis wiedii	Margay
Felis yagouaroundi	Jaguarundi
Felis lynx	Lynx
Felis rufus	Bobcat

ORDER MYSTICETI—Baleen Whales

FAMILY ESCHRICHTIIDAE—Gray Whale

Eschrichtius robustus	Gray Whale

FAMILY BALAENOPTERIDAE—Rorquals

Balaenoptera acutorostrata	Minke Whale
Balaenoptera borealis	Sei Whale
Balaenoptera edeni	Bryde's Whale
Balaenoptera physalus	Fin Whale
Balaenoptera musculus	Blue Whale
Megaptera novaeangliae	Humpback Whale

FAMILY BALAENIDAE—Right Whales

Balaena glacialis	Black Right Whale
Balaena mysticetus	Bowhead Whale

ORDER ODONTOCETI—Toothed Whales

FAMILY MONODONTIDAE—Monodontids

Delphinapterus leucas	White Whale or Beluga
Monodon monoceros	Narwhal

FAMILY DELPHINIDAE—Delphinids

Steno bredanensis	Rough-toothed Dolphin
Tursiops truncatus	Bottle-nosed Dolphin
Stenella frontalis	Bridled Spotted Dolphin
Stenella attenuata	Pantropical Spotted Dolphin
Stenella plagiodon	Atlantic Spotted Dolphin
Stenella coeruleoalba	Striped Dolphin
Stenella clymene	Short-snouted Spinner Dolphin
Stenella longirostris	Long-snouted Spinner Dolphin
Delphinus delphis	Saddle-backed Dolphin
Lagenorhynchus albirostris	White-beaked Dolphin
Lagenorhynchus acutus	Atlantic White-sided Dolphin
Lagenorhynchus obliquidens	Pacific White-sided Dolphin
Grampus griseus	Risso's Dolphin or Grampus
Feresa attenuata	Pygmy Killer Whale
Pseudorca crassidens	False Killer Whale
Globicephala melaena	Long-finned Pilot Whale
Globicephala macrorhynchus	Short-finned Pilot Whale
Orcinus orca	Killer Whale
Lissodelphis borealis	Northern Right-whale Dolphin

FAMILY PHOCOENIDAE—Porpoises

Phocoena phocoena	Harbor Porpoise
Phocoenoides dalli	Dall's Porpoise

FAMILY ZIPHIIDAE—Beaked Whales

Berardius bairdii	North Pacific Bottle-nosed Whale
Ziphius cavirostris	Goose-beaked Whale
Hyperoodon ampullatus	North Atlantic Bottle-nosed Whale
Mesoplodon hectori	Hector's Beaked Whale
Mesoplodon mirus	True's Beaked Whale
Mesoplodon europaeus	Gervais' Beaked Whale
Mesoplodon ginkgodens	Ginkgo-toothed Whale
Mesoplodon carlhubbsi	Arch-beaked Whale
Mesoplodon stejnegeri	Bering Sea Beaked Whale
Mesoplodon bidens	North Atlantic Beaked Wha
Mesoplodon densirostris	Dense-beaked Whale

FAMILY PHYSETERIDAE—Sperm Whales

Kogia simus	Dwarf Sperm Whale
Kogia breviceps	Pygmy Sperm Whale
Physeter macrocephalus	Sperm Whale

ORDER SIRENIA—Sea Cows

FAMILY TRICHECHIDAE—Manatees

Trichechus manatus	Manatee

ORDER ARTIODACTYLA—Even-toed Ungulates

FAMILY SUIDAE—Pigs

*Sus scrofa**	Wild Pig

FAMILY TAYASSUIDAE—Peccaries

Tayassu tajacu	Collared Peccary

FAMILY CERVIDAE—Cervids

Cervus elaphus	Wapiti or Elk
*Cervus dama**	Fallow Deer
Odocoileus hemionus	Mule Deer
Odocoileus viginianus	White-tailed Deer
Alces alces	Moose
Rangifer tarandus	Caribou

FAMILY ANTILOCAPRIDAE—Pronghorn

Antilocapra americana	Pronghorn

FAMILY BOVIDAE—Bovids

Bison bison	Bison
Oreamnos americanus	Mountain Goat

Ovibos moschatus	Muskox
Ovis canadensis	Mountain Sheep
Ovis dalli	Dall's Sheep
*Ammotragus lervia**	Barbary Sheep

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A NEW SPECIES OF TUBE-NOSED FRUIT BAT (*NYCTIMENE*) FROM THE BISMARCK ARCHIPELAGO, PAPUA NEW GUINEA

JAMES DALE SMITH AND CRAIG S. HOOD

Tube-nosed fruit bats of the genus *Nyctimene* (Chiroptera, Megachiroptera, Pteropodidae), and its sister-taxon *Paranyctimene*, are unique among the various taxa that comprise the family Pteropodidae, being distinguished by their peculiar tubular nostrils. The nine currently recognized species of *Nyctimene* occur in Indo-Australia from Timor, through Sulawesi and the Moluccas, New Guinea and tropical Australia, and the Bismarck and Solomon Islands to Santa Cruz Island.

In the summer of 1979, the Taylor South Seas Expedition from the Natural History Museum of Los Angeles County (LACM), led by one of us (Smith), visited the Bismarck Islands of New Ireland and New Britain for the purpose of surveying the bat fauna of this poorly known region. Preliminary results of this expedition were reported by Smith and Hood (1981). A more extensive report of collections made, plus the results of a second expedition (1981) to the Bismarcks (including Manus and Duke of York islands), is in progress. In addition to the capture of many species new to the fauna of the Bismarcks, we encountered an undescribed species of *Nyctimene*, which is diagnosed and discussed below.

Nyctimene masalai, new species

Demonic Tube-nosed Fruit Bat

Holotype.—LACM 65798, adult male (preserved in alcohol, skull removed) collected on 9 July 1979 by James Dale Smith (original number 4522) at Ralum, 10 m., New Ireland Island, New Ireland Prov., Papua New Guinea (lat. 3° 33′ S, long. 152° 22′ E).

Paratype.—LACM 65799, young adult male (preserved in alcohol, skull removed) collected on 19 July 1979 by James Dale Smith (original number 4878) at 2 km. NW Hilalon, sea level, New Ireland Island, New Ireland Prov., Papua New Guinea (lat. 3° 51′ S, long. 152° 39′ E).

Distribution.—Bismarck Archipelago, Papua New Guinea, known only from New Ireland Island.

Diagnosis.—Size moderately large (see measurements below). Color mottled, dark reddish brown above; black, middorsal strip (5 mm. wide) from back of crown to base of tail; grayish white with yellowish brown wash below; spots on wings, ears, and narial tubes whitish. Cranium narrow and elongate (rectangular rather than squarish); rostrum relatively long and narrow; frontal sinuses inflated and parallel to each other (not converging in supraorbital region); maxillary toothrows straight, converging anteriorly; bony palate moderately domed (not flat), deepest anterior to second upper premolars; postdental palate not markedly pandurate; pterygoid wings low. Dentition with marked reduction of coronal cusps; canines relatively short and broad-based, upper pair lacking labial cusps; P3 and p3 unicuspid and nearly subconical.

Measurements.—Selected cranial and external measurements (in mm.) of holotype and paratype, respectively: condylobasal length, 30.7, 29.7; zygomatic breadth, 20.4, 20.9; mastoid breadth, 13.7, 13.5; interorbital breadth, 6.2, 5.7; breadth across canines, 5.6, 5.8; length of maxillary toothrow, 10.9, 10.4; breadth across upper molars (M1-M1), 8.3, 9.0; length of mandibular toothrow, 12.5, 12.1; length of mandible, 24.0, 23.4; height of coronoid process, 13.3, 13.7; length of head and body, 103, 94; length of tail, 22, 21; length of hind foot, 14, 13; length of ear, 14, 14; length of forearm, 67.5, 63.5; weight (grams), 52.3, 45.2.

Description.—Head long and narrow; face deep; ears broad, bluntly pointed; narial tubes long, directed anteriorly; flight membranes dark brown; wing attached to dorsal surface of foot at base of third toe; large white blotches on dorsal surface of forearm and all digits of wing (spots on membrane between fingers pale yellowish brown); leading edge of ear pinna and narial tube with white spots.

Pelage and Coloration.—Dorsal pelage long (8-9 mm.) and lax; extending along pectoral limb to proximal third of forearm and

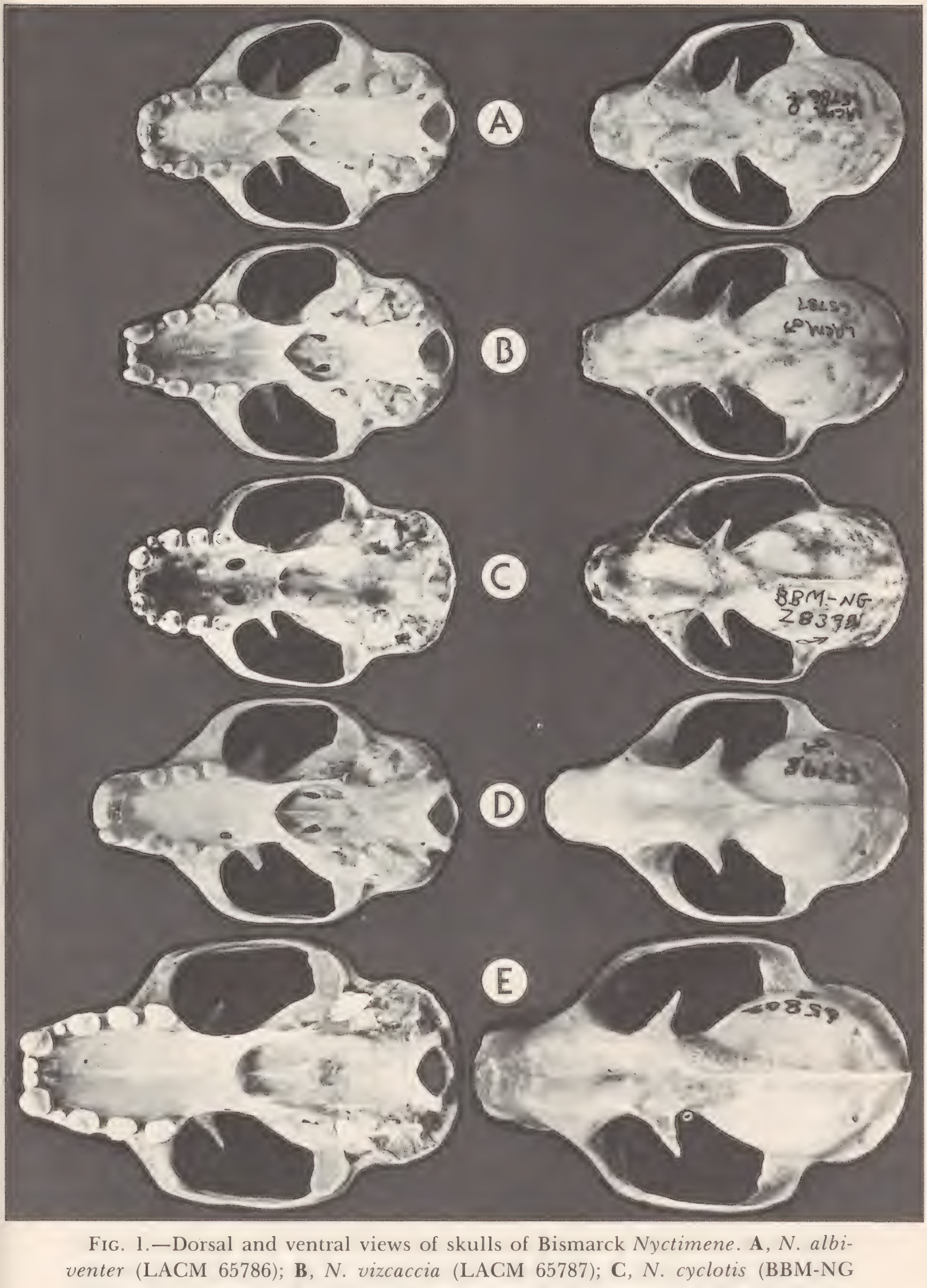

FIG. 1.—Dorsal and ventral views of skulls of Bismarck *Nyctimene*. **A**, *N. albiventer* (LACM 65786); **B**, *N. vizcaccia* (LACM 65787); **C**, *N. cyclotis* (BBM-NG 28398); **D**, *N. masalai* (LACM 65798, holotype); **E**, *N. major* (LACM 65802). See text for discussion.

also extending to knees in a V-shaped pattern with apex at base of tail; hairs tricolored (dark brown at base, mid-region pale grayish brown, reddish brown at tip); overall coloration of back mottled dark reddish brown; dark black middorsal stripe (5 mm. wide) from back of crown to base of tail. Ventral pelage short (4-5 mm.) and sparse; throat and middle portion of chest and abdomen grayish white; lateral regions and lower flanks with yellowish brown wash.

Cranium.—Rostrum relatively short and narrow (Fig. 1D); breadth across lacrimal foramina only slightly greater than width of rostrum and interorbital region; braincase long and narrow (not globose); zygomatic arches flared to the side, straight for most of their length and paralleling longitudinal axis of cranium. The foregoing features give the cranium a roughly rectangular shape (viewed from above). Frontal sinuses inflated and lying parallel to each other, not converging appreciably in supraorbital region, and separated by a medial groove; sagittal and lambdoidal crest low. Viewed in profile, skull rather planar (Fig. 2B); rostral portion of nasals flattened; forehead rising with a gentle angle to supraorbital boss; top of skull flat to about middle of braincase, then gently curved ventrally; braincase not deflected below alveolar plane. Bony palate long and narrow; gently domed, deepest portion anterior to second upper premolars; postdental palate not markedly pandurate; pterygoid wings low (Fig. 2B); maxillary toothrows straight (not bowed or arcuate), converging anteriorly.

Dentition.—Dental formula I 2/0, C 1/1, P 3/2, M 1/2 = 24.

Incisors. Upper incisors tightly placed between upper canines; each subtriangular with a strong central cusp; narrow cingular shelf on posterior face extending to anterolateral face of tooth. Lower incisors absent as is characteristic of all members of the genus.

Canines. Upper canines relatively short; posterior cingular shelf confined to internal, basal portion of tooth (Fig. 3A); labial margin of cingulum with shallow notch (this may be exaggerated as tooth wear progresses); external cusp, or indication thereof, absent; rear face of canine flat. Lower canines short, broad at base; posterior cingulum extending rearward from middle of labial margin as a gently spiralled scallop to internal apex of canine.

Premolars. First upper premolar (P2) reduced to small spicule; coronal surface generally round and flat; second upper premolar (P3) most prominent of postcanine teeth; single strong

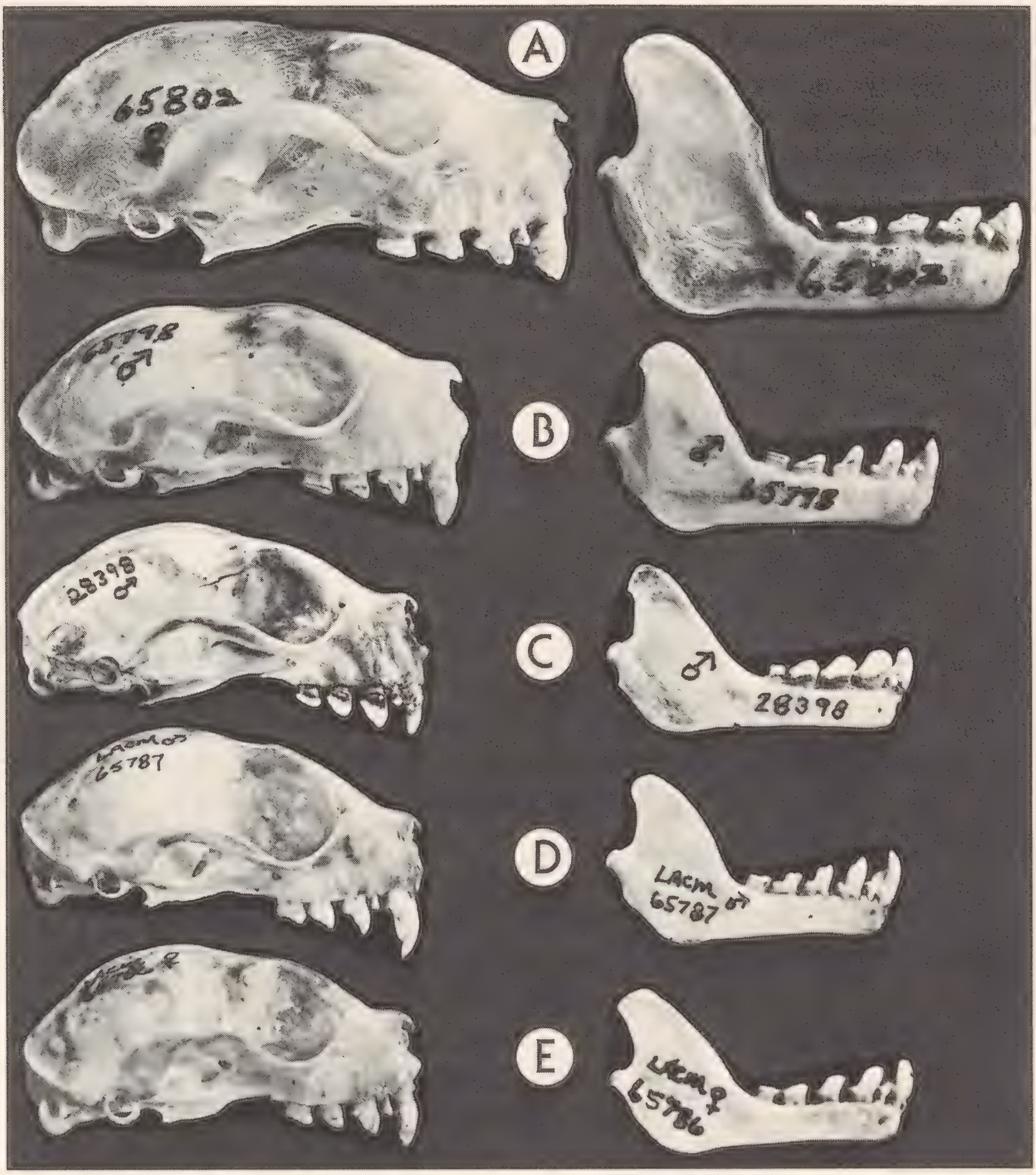

FIG. 2.—Profile of skull and lower jaw of Bismarck *Nyctimene*. **A**, *N. major* (LACM 65802); **B**, *N. masalai* (LACM 65798, holotype); **C**, *N. cyclotis* (BBM-NG 28398); **D**, *N. vizcaccia* (LACM 65787); **E**, *N. albiventer* (LACM 65786). See text for discussion.

cusp on anterior, external portion of tooth (Fig. 3A); internal cusp absent (perhaps it has fused completely with main cusp); short labial and lingual ridges extending rearward from central cusp, then dropping abruptly to shelflike heel of tooth; third upper premolar (P4) subequal in size to P3; strong anterior, external cusp; lower anterior, internal cusp; lobate heel angled lingually. First lower premolar (p2) reduced in size; crown generally flat and with short external cusp; second lower premolar (p3) with strong, high cusp on anterior, external portion of tooth

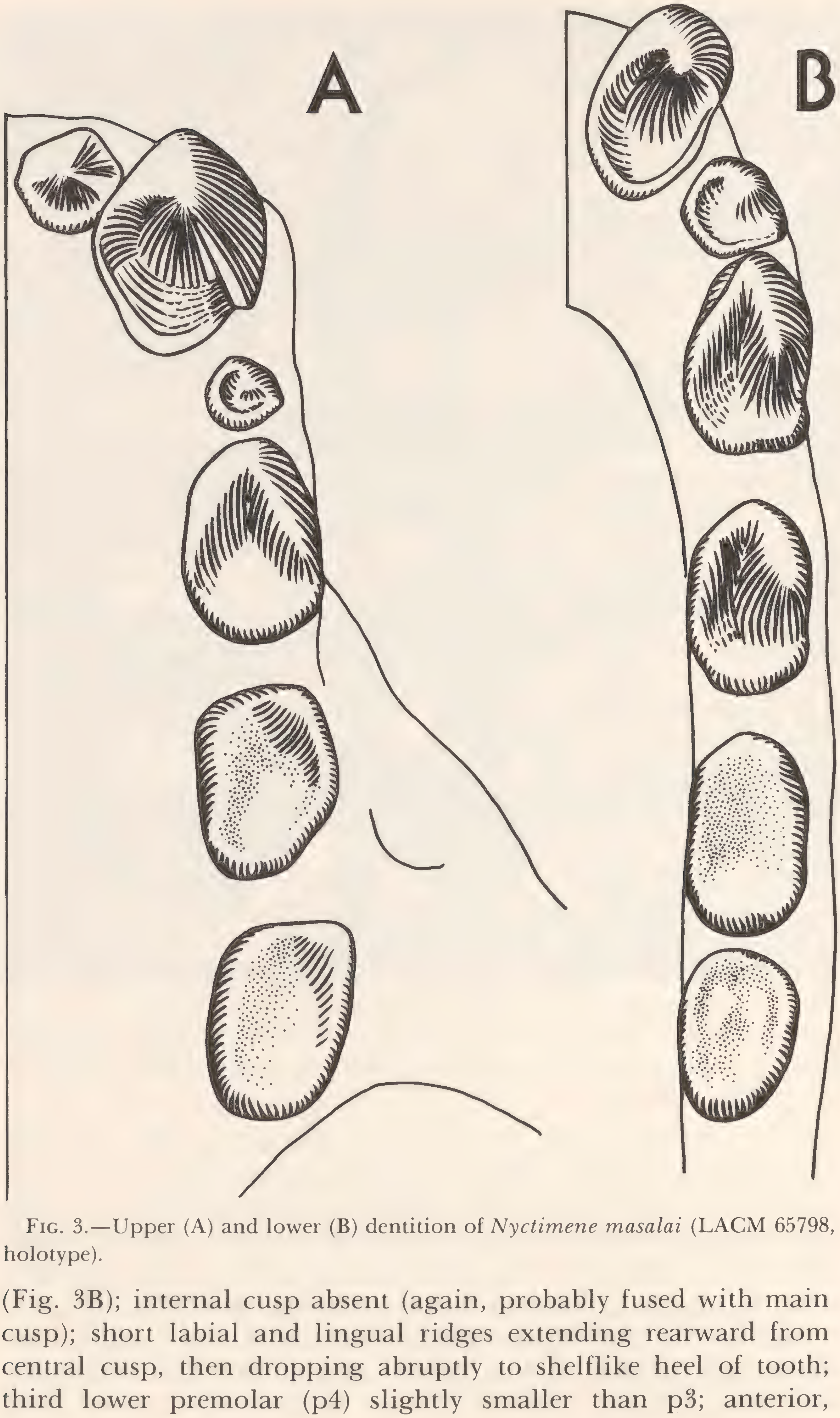

Fig. 3.—Upper (A) and lower (B) dentition of *Nyctimene masalai* (LACM 65798, holotype).

(Fig. 3B); internal cusp absent (again, probably fused with main cusp); short labial and lingual ridges extending rearward from central cusp, then dropping abruptly to shelflike heel of tooth; third lower premolar (p4) slightly smaller than p3; anterior, external cusp high; internal cusp not distinct; these two cusps connected by a ridge that arcs around anterior margin of tooth; posteriorly, internal and external ridges drop rather abruptly to heel of tooth.

Molars. First and only upper molar (M1) subequal in size to P4; cusp positions and ridges similar to those of P4 but much lower; tooth nearly flat as viewed in profile. First lower molar (m1) similar to p4 in size and coronal morphology; anterior portion of tooth only slightly higher than heel; second lower molar (m2) slighly shorter than m1; no distinct cusps apparent, crown flat.

Soft palate.—Entire length of soft palate covered with 20-21 palatal ridges, eight or nine of which are interdental; first ridge short, extending straight across palate between first upper premolars; second through fifth or sixth ridges similar in shape with a lateral branch extending anteriorly from toothrow at about 45° angle, then bending sharply to cross midline at perpendicular angle; next few ridges with indentation medially, may connect at midline; all aforementioned ridges rather thick, rounded, and separated by deep grooves, their surface wrinkled. Posterior to interdental ridges is a series of more widely spaced, delicate ridges clothed by many sharply pointed, toothlike papillae, anteriormost of which randomly and irregularly traverse soft palate; many do not reach midline; last eight or nine postdental ridges more or less regular in form, spacing, and nearly all extend, unbroken, across soft palate.

Etymology.—The epithet for the new species, *masalai*, is taken from the Tolai language and means forest demon or devil.

Comparison and Discussion

The most recent critical review of the tube-nosed fruit bats is that by Andersen (1912*b*:681-722, 828). He treated 13 species of *Nyctimene* (*papuanus*, *albiventer*, *minutus*, *varius*, *cyclotis*, *cephalotes*, *geminus*, *major*, *scitulus*, *lullulae*, *aello*, *robinsoni*, and *certans*). The holotypes of these, except for *cephalotes* (not examined by Andersen and apparently lost), are housed in the collection of the British Museum (Natural History). All except *N. cephalotes* (Pallas, 1767), *N. albiventer* (Gray, 1862), *N. major* (Dobson, 1877), *N. aello* (Thomas, 1900), *N. robinsoni* Thomas, 1904, *N. major lullulae* Thomas, 1904, and *N. certans* Andersen, 1912*a* were described by Andersen (1910). Since the review by Andersen (1912*b*), seven additional taxa of *Nyctimene* have been described: *N. vizcaccia* Thomas, 1914, *N. draconilla* Thomas, 1922*a*, *N. celaeno* Thomas, 1922*b*, *N. sanctacrucis* Troughton, 1931, *N. bougainville* Troughton, 1936, *N. malaitensis* Phillips, 1968, and *N. albiventer minor* Phillips, 1968. *Paranyctimene raptor* Tate, 1942, also was described after Andersen (1912*b*). Tate (1942: 341-343) discussed some, but not all, of these taxa in his account of pteropodids contained in the Archbold collections. Likewise, Laurie and Hill (1954: 46-48) treated most, but not all, of these bats. They assigned the various taxa of *Nyctimene* known to occur in the geographic area covered by them to species and subspecies, but did not discuss or otherwise justify these assignments. More recently, several other workers (Phillips, 1968:817-825; McKean, 1972:16-20; and Koopman, 1979:12) have remarked on regionally limited taxa of *Nyctimene*. To date, however, the genus remains unreviewed in its entirety.

Like many bats from the Indo-Australian region, most species of *Nyctimene* are represented only by the holotype or extremely small series (one or two in most cases) from scattered localities, many of which are islands. In addition, much of the crucial cranial material is damaged or has heavily worn dentition, thereby limiting critical comparisons and analyses of characters. These troublesome factors are further aggravated by a rather high degree of individual variability that is apparently common among pteropodid bats. In the past, species of *Nyctimene* have been based mostly on coloration and overall size. In preparing the description on *N. masalai*, we have examined and directly compared it with the 15 holotypes of *Nyctimene* in the British Museum (Natural History), holotypes of *N. malaitensis* and *N. albiventer minor* (Bernice P. Bishop Museum, Honolulu), and representative series of all other species of *Nyctimene* except *N. sanctacrucis*. In addition, we have attempted to identify and use characteristics in the diagnosis and description that seem applicable to all taxa of *Nyctimene*.

Nyctimene masalai is easily distinguished from *N. m. major*, with which it is sympatric, on the basis of large overall size of the latter (Figs. 1E and 2A). The cranium of *major* is flatter in profile, much more massive, and the dentition is characteristically more cuspidate than that of *masalai* (Fig. 1E). *Nyctimene masalai* approaches *N. m. scitulus* in overall size, but remains distinct because of the qualitative characters mentioned above. This is also the case with *N. geminus*, which currently is regarded as a geographic race of *major*. *Nyctimene lullulae* (also regarded as a subspecies of *major*) is slightly smaller than *masalai*, but again, is distinguished by cranial and dental features typical of *major*. *Nyctimene robinsoni*, *N. aello*, and *N. celaeno* (regarded as a race of *aello* by Laurie and Hill, 1954) occupy geographic ranges that are allopatric to that of *N. masalai*. *Nyctimene robinsoni*, an apparently close relative of *N. major*, is distinguished from *masalai* by the same general suite of characters that separates *masalai* from *major*. Large size, highly cuspidate dentition, and a unique broad middorsal stripe easily separate *N. aello* and *N. celaeno* from *N. masalai*.

Nyctimene masalai is slightly larger in overall size compared to *N. cyclotis* (Figs. 1C and 2C). It is conceivable that these two occur sympatrically (*cyclotis* having been recently reported from New Britain Island by Smith and Hood, 1981), but as yet they remain allopatric. While similar in size, *cyclotis* is readily identified by its generally dark, extremely long and wooly pelage, as well as uniquely cuspidate postcanine dentition (Fig. 1C). The premolars and molars of *cyclotis* are round as opposed to rectangular and the premolars have three strong cusps; the palate is markedly arcuate. The cranium of *cyclotis* tends to be more squarish than rectangular. The large round palatal fenestrations shown in Fig. 1C are not wholly artifactual, but are frequently encountered in specimens of *cyclotis*, and are often asymmetrical. They do not occur in all specimens, but their form, position, and incidence of occurrence seem consistent enough to consider them a feature of the species.

The two remaining species that occur in sympatry with *N. masalai* are *N. albiventer* and *N. cephalotes*. They are similar in size, but both are smaller than *masalai*. The Bismarck Archipelago (including the Admiralty Islands) is the only geographic area in which *albiventer* and *cephalotes* are known to occur sympatrically. *Nyctimene albiventer*, in its current context, is a wide-ranging species that occurs from the northern Moluccas through New Guinea, the Bismarcks and the Admiralties, to the Solomon Islands. Laurie and Hill (1954) placed *N. papuanus*, *N. draconilla*, and *N. bougainville* as subspecies of *N. albiventer*. With the exception of *bougainville* (see below), these associations seem to be correct, although Koopman (1979:6) regarded *draconilla* as a distinct species (the specimens referred to *draconilla* by Greig-Smith, 1975, and mentioned by Koopman, 1979, as partial justification of this arrangement, are *Paranyctimene raptor*). The name *cephalotes* was first introduced into the Bismarck area when

Laurie and Hill (1954) relegated *N. vizcaccia* Thomas, 1914, to subspecific status under *N. cephalotes*. Formerly, *cephalotes* was applied to bats that occurred generally west of New Guinea (Timor, Peleng Island, off the east coast of Sulawesi, and the Moluccas); one specimen from Numfoor Island, Geelvinck Bay, Irian Jaya, was also assigned to *cephalotes* (Laurie and Hill, 1954; Koopman, 1979).

In the preparation of this description of *masalai* and the development of comparative criteria for species of *Nyctimene*, we stumbled inadvertently onto a problem concerning the identity of *albiventer* and *cephalotes*. Neither *albiventer* nor *cephalotes* is especially well defined in the literature and, as noted above, the holotype of the latter appears to be lost. We arrived at our understanding of *cephalotes* by first defining the nature of *albiventer*. For this, we used the holotypes of *albiventer*, *papuanus*, and *draconilla* as well as considerable comparative material from the mainland of New Guinea. We regard *albiventer* to be a moderately small species with a narrow, brownish black middorsal strip. The dorsal pelage is not mottled and the venter is generally uniformly whitish or yellowish white. The cranium is squarish with an extremely short rostrum and globose braincase (Figs. 1A and 2E), and the palate and maxillary toothrow are broad and arcuate rather than narrow, straight-sided, and convergent anteriorly. The second upper premolar is bicuspidate with a strong external cusp and a lower, usually prominent, internal cusp (Fig. 1A), but tooth wear may obliterate the internal cusp. The second lower premolar also is cuspidate with a strong external cusp, usually flanked by a short anterior and posterior loph, and a prominent internal cusp. There is some individual variation in the distinctness of the internal cusp throughout the geographic range of the species and wear quickly obliterates its appearance. However, this tooth and its upper counterpart are always broad and round rather than long and narrow. All of these features easily distinguish *albiventer* from *masalai*. They do not, however, characterize tube-nosed fruit bats from the Solomon Islands that have been previously assigned to *N. albiventer bougainville*.

With *albiventer* so defined, we are left with one remaining species in the Bismarcks—supposedly *N. cephalotes*. This bat agrees in size and general external appearance with *albiventer*, but its dorsal pelage is usually mottled and the venter is often darker. In describing *N. bougainville*, Troughton (1936) made similar observations in his comparison with *N. papuanus*, and these appear to have influenced Pohle's (1953) association of *bougainville* with *albiventer*. Subsequent authors have followed this assignment. More importantly, the cranium and dentition of the remaining taxon differ considerably from those of the form that we regard as *albiventer*. The cranium is rectangular with a relatively longer rostrum than in *albiventer*, and the braincase is elongate, not globose (Fig. 1B). The second upper and lower premolars lack a distinct internal cusp. Often there is a marked, flangelike ridge sweeping in a graceful and gentle curve from the posterior internal margin of the cingulum upward to the apex of the prominent and narrow external cusp (Fig. 1B). This is especially apparent on unworn teeth. The teeth are usually longer and somewhat narrower than those of *albiventer*, although this tendency may be obscured by wear and erosion. The preceding features characterize specimens formerly referred to *N. albiventer bougainville* from the Solomon Islands, the holotype of *N. vizcaccia*, and a larger series of topotypes (Ruk, Rooke, or Umboi Island) in the Bernice P. Bishop Museum.

Finally, we compared the Bismarck and Solomon specimens with those referred to *cephalotes* from Peleng Island and the Moluccas. The latter agree in external appearance and general shape of the cranium. The crania of Bismarck and Solomon specimens tend to be less rectangular than either those of *cephalotes* or *masalai*. Specimens of *cephalotes* from Peleng Island and the Moluccas are larger in overall size, and the upper and lower premolars have a moderately prominent internal cusp. This is also true of the specimen from Numfoor. On the lower premolar, this cusp may be reduced to a promontory or shoulder on the internal ridge that extends from the posterior cingulum to the apex of the external cusp. Thus, given these differences, we regard *Nyctimene vizcaccia* Thomas (1914) to be a valid species, separate and distinct from *cephalotes* and *masalai*, and occupying a geographic range in the Bismarck and Solomon Islands. All three taxa appear to be allied and may ultimately be regarded as members of a "*cephalotes*-group." Furthermore, we regard *N. bougainville* from the Solomon Islands, heretofore assigned to *N. albiventer*, as a junior synonym of *N. vizcaccia* and as a valid subspecies of that species, *Nyctimene vizcaccia bougainville*, new combination. There seems to be little evidence to warrant recognition of the subspecies *minor* from Fauro, Choiseul, and Santa Ysabel islands. Although slightly smaller in overall size, representative specimens are not markedly removed from the range of variation in *N. v.*

bougainville, and we therefore regard *N. albiventer minor* as a junior synonym of *N. v. bougainville.*

Nyctimene masalai differs from supposed *cephalotes* from Peleng Island and the Moluccas by being larger in overall size, having a somewhat broader, yet rectangular cranium, and a relatively longer rostrum. The dentition of *masalai* is, perhaps, the most reduced of any species of *Nyctimene* in terms of coronal cuspidation (Fig. 3). *Nyctimene malaitensis* Phillips (1968) is known only from the type specimen from Malaita Island, Solomon Islands. It appears to be a species distinct from *N. v. bougainville* which is smaller in all respects. *Nyctimene malaitensis* does approach *masalai* in size, but the cranium is less rectangular, the rostrum is shorter and broader, and the palate is flat, not domed as in *masalai*. The dentition of the holotype of *malaitensis* is badly worn. The foundations of the teeth are broad and rounded, and those of the upper and lower second premolars appear to have supported internal cusps.

SUMMARY

A new species, *Nyctimene masalai*, is described from New Ireland Island, Bismarck Archipelago, Papua New Guinea. The new species is compared with all other species of *Nyctimene* except *N. sanctacrucis*. In these comparisons, useful characteristics for identifying the species of *Nyctimene* are presented, and *Nyctimene albiventer* and *N. cephalotes* are discussed in detail. As a result, *Nyctimene vizcaccia* is raised to species rank. *Nyctimene bougainville*, from the Solomon Islands (previously assigned to *N. albiventer*), is placed as a junior synonym of *N. vizcaccia*, and Solomon representatives are assigned to *Nyctimene vizcaccia bougainville*. *Nyctimene albiventer minor*, also from the Solomons, is put into the synonymy of *N. vizcaccia bougainville.*

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REVIEW OF THE WHITE-FOOTED MICE, GENUS PEROMYSCUS, OF NICARAGUA

J. Knox Jones, Jr., and Terry L. Yates

White-footed mice of the genus *Peromyscus* have the broadest distribution in North America of any of the New World cricetine genera, occurring from north-central Canada southward to Panamá (and barely into South America). Radiation in this diverse group has been especially pronounced in southern México and adjacent parts of Central America, and this situation, while not yet fully understood, has been the subject of several recent studies. Nevertheless, virtually nothing is known of distribution and variation in the *Peromyscus* of Nicaragua, the subject of the present paper.

In the first of two publications on collections of mammals from Nicaragua, J. A. Allen (1908:658) named and described "*Peromyscus nicaraguae*," based on a holotype and other specimens from Matagalpa, but including also material from San Rafael del Norte, Ocotal, Volcán de Chinandega, and Chontales. In the second paper (1910:100), Allen listed additional material from Matagalpa and San Rafael del Norte as well as from the new localities of Peña Blanca, Río Coco, and Uluse. However, in his monographic study of the genus, Osgood (1909:203) placed *P. nicaraguae* in the synonymy of *Peromyscus mexicanus saxatilis* Merriam, wherein it has remained (Hall, 1981:711). Until now, *P. mexicanus* has been the only species of *Peromyscus* reported from Nicaragua.

In the winter and spring of 1956, J. R. Alcorn and his family obtained mammals in Nicaragua for the Museum of Natural History at the University of Kansas. Subsequently, between February 1964 and the spring of 1968, several other field parties from Kansas, supported by a contract (DA-49-193-MD-2215) to one of us (Jones) from the U.S. Army Medical Research and Development Command, collected both mammals and their ectoparasites in Nicaragua. Furthermore, L. G. Clark, then associated with the University of Pennsylvania, collected mammals in that country in connection with studies of leptospirosis; his material was divided between the Museum of Natural History at Kansas and the U.S. National Museum of Natural History.

Among the specimens accumulated as a result of these endeavors were more than 400 individuals of *Peromyscus* representing three species as currently understood (Huckaby, 1980). Two of these, *P. gymnotis* and *P. stirtoni,* are new to the known fauna of Nicaragua.

METHODS AND MATERIALS

All specimens listed as examined are in the University of Kansas Museum of Natural History, and catalogue numbers relate to that collection. Measurements are given in millimeters. Those of the cranium were taken as described by Hooper (1952) to the nearest 0.1 millimeter by means of dial calipers. External measurements were taken directly from museum specimen labels.

For *Peromyscus mexicanus* and *P. gymnotis,* individual, age, and secondary sexual variation was analyzed with the statistical analysis system (SAS) designed and implemented by Barr *et al.* (1976). All specimens were assigned to one of six age classes following the technique used by Schmidly (1972). Means were calculated for each character, and a one-way analysis of variance was used to test for differences among age classes and between sexes. Duncan's multiple range test was used to identify maximally nonsignificant subsets. Coefficients of variation (CV) were calculated to determine the extent of variability for each character.

Geographic variation was analyzed by means of univariate (mean, standard deviation, standard error) and multivariate statistics. The latter consisted of a multivariate analysis of variance (MANOVA) in SAS (see Yates *et al.,* 1979). *Peromyscus stirtoni* was not included in these analyses because so few specimens were available for study.

Because undue crowding of symbols would have resulted, some localities from which specimens are known were not plotted on the distribution map. These localities are indicated in italic type in the accounts that follow.

Statistical Analyses

Nongeographic variation owing to sex and age was examined prior to analysis of geographic variation. Single-classification analysis of variance was used to test each of 15 external and cranial characters in selected samples of *Peromyscus mexicanus* and *P. gymnotis* to ascertain if any significant morphological differences were related to sex. No differences of significance were found between sexes for any measurement; thus males and females were considered together in all subsequent analyses. Likewise, analysis of variance among age classes of both species revealed no consistent significant differences among specimens categorized in age classes 3 through 6 (Table 1), and all mice in these age classes were treated as adults for further statistical analysis. Actually, most of our samples (as in Table 1) contained adults classified only in age classes 3 to 5.

In order to determine the extent of variation among samples and between species with all cranial characters considered simultaneously, a multivariate analysis of variance was used. Samples of *P. mexicanus* and *P. gymnotis* (Fig. 1) were analyzed together, based on 10 cranial measurements, in an effort to assess the relative degree of morphological distinctness between the two in addition to assessing geographic variation within each species. Because of a relatively high level of variability and some missing data, external measurements and zygomatic breadth were excluded from the multivariate portion of the analysis.

The variance-covariance matrix yielded canonical variates based on the 10 characters used in the study. The first vector expressed 61.45 per cent of the phenetic variation whereas vector two expressed an additional 12.64 per cent. A two-dimensional plot of vector one against vector two (Fig. 2) revealed two clusters of samples. The first cluster consisted of samples of *P. gymnotis* from western Nicaragua (departments of Chinandega, Managua, Carazo, Granada, and Rivas). The second cluster consisted of samples of *P. mexicanus* from the departments of Estelí, Jinotega, and Matagalpa, and from Isla de Ometepe.

The contributions of each character to the first two canonical variates are presented in Table 2. Greatest length of skull and breadth of braincase exerted the heaviest influence on the first vec-

TABLE 1.—*Results of analysis of variance among age classes in external and cranial measurements in a selected sample of* Peromyscus gymnotis *from the vicinity of Diriamba, Carazo, Nicaragua. Statistics given are sample size, mean, and* F. *Results of Duncan's multiple range test are also given. Means connected by a vertical bar are not significantly different at* $P < .05$. *Groups of means that were found not to be significantly different are marked* NS.

Measurements and age classes	*N*	Mean	*F*	Results Duncan MRT			
Total length							
IV	21	227.7	29.0	│			
V	2	226.0		│			
III	24	221.9		│	│		
II	3	210.0			│		
I	4	171.0				│	
Length of tail							
V	2	117.0	16.6	│			
IV	21	115.2		│			
III	24	111.9		│			
II	3	107.3		│			
I	4	87.0			│		
Length of hind foot							
IV	22	24.2	1.3	NS			
III	25	24.1					
I	4	23.5					
II	3	23.3					
V	2	23.0					
Length of ear							
V	2	19.5	2.9	│			
IV	21	19.0		│			
III	22	18.8		│			
II	3	17.7			│		
I	4	17.0			│		
Greatest length of skull							
IV	24	30.6	21.1	│			
V	2	30.1		│	│		
III	27	29.9			│		
II	3	28.5				│	
I	2	25.6					│
Zygomatic breadth							
V	2	15.2	31.1	│			
IV	22	15.1		│			
III	22	14.8		│			
II	3	13.9			│		
I	4	11.8				│	

TABLE 1.—*Continued.*

Interorbital breadth						
V	2	4.9	0.5	NS		
III	29	4.9				
IV	25	4.9				
I	4	4.8				
II	3	4.8				
Breadth of braincase						
V	2	13.4	2.5	│		
IV	26	13.3		│		
II	3	13.2		│	│	
III	29	13.1		│	│	
I	2	12.5			│	
Depth of braincase						
V	2	10.0	1.0	NS		
IV	26	9.9				
III	29	9.9				
II	3	9.7				
I	2	9.5				
Length of rostrum						
V	2	12.2	10.3	│		
IV	24	12.0		│		
III	29	11.9		│		
II	3	11.0			│	
I	3	10.3			│	
Length of palate						
V	2	4.6	2.3	NS		
IV	24	4.5				
III	29	4.4				
II	3	4.3				
I	4	4.2				
Length of maxillary toothrow						
V	2	4.5	8.6	│		
IV	26	4.5		│		
III	29	4.5		│		
II	3	4.4		│		
I	4	4.1			│	
Length of incisive foramen						
IV	26	6.1	26.3	│		
III	29	5.8			│	
V	2	5.8			│	
II	3	5.5			│	
I	4	4.4				│

TABLE 1.—*Continued.*

Breadth of zygomatic plate						
V	2	2.6	5.0	│		
IV	26	2.3			│	
III	29	2.3			│	
I	4	2.1				│
II	3	2.0				│
Breadth of rostrum						
IV	26	5.4f	14.6	│		
V	2	5.3		│		
III	29	5.3		│	│	
II	3	4.9			│	
I	3	4.3				│

tor. Length of maxillary toothrow exerted the greatest influence on the second. Thus, the first vector tended primarily to separate individuals with longer, broader skulls (*P. mexicanus*) from those with shorter, narrower skulls (*P. gymnotis*). Vector two tended to separate samples within each of the two major clusters from each other although no major subclusters were evident. When sample means were plotted along vector one, those of *gymnotis* (samples 1, 8, 9, 10, 12) from western Nicaragua all fell along coordinates from 3.59 to 3.68 (Fig. 2), whereas samples of *mexicanus* (2, 3, 4, 5, 6, 7, 11) fell along coordinates from 3.76 to 3.90. When all individuals were plotted, however, some overlap occurred between the extremes (that is, the edges of the two major clusters overlapped). We recognize these two taxa as distinct at the specific level following Musser (1971) and Huckaby (1980), although much remains to be learned concerning their precise systematic relationships. The intermediate nature of individuals in samples 2, 3, and 7 (Fig. 2) suggests the possibility that hybridization between the two may occur in north-central Nicaragua, for example, and that *gymnotis* and *mexicanus* thus may be conspecific. We thank Michael D. Carleton for verifying our initial identify of the smaller of these species as *P. gymnotis*.

ACCOUNTS OF SPECIES

Peromyscus gymnotis Thomas, 1894

Distribution in Nicaragua.—Pacific lowlands and isolated volcanos of western Nicaragua southward to Costa Rican border (Fig. 3).

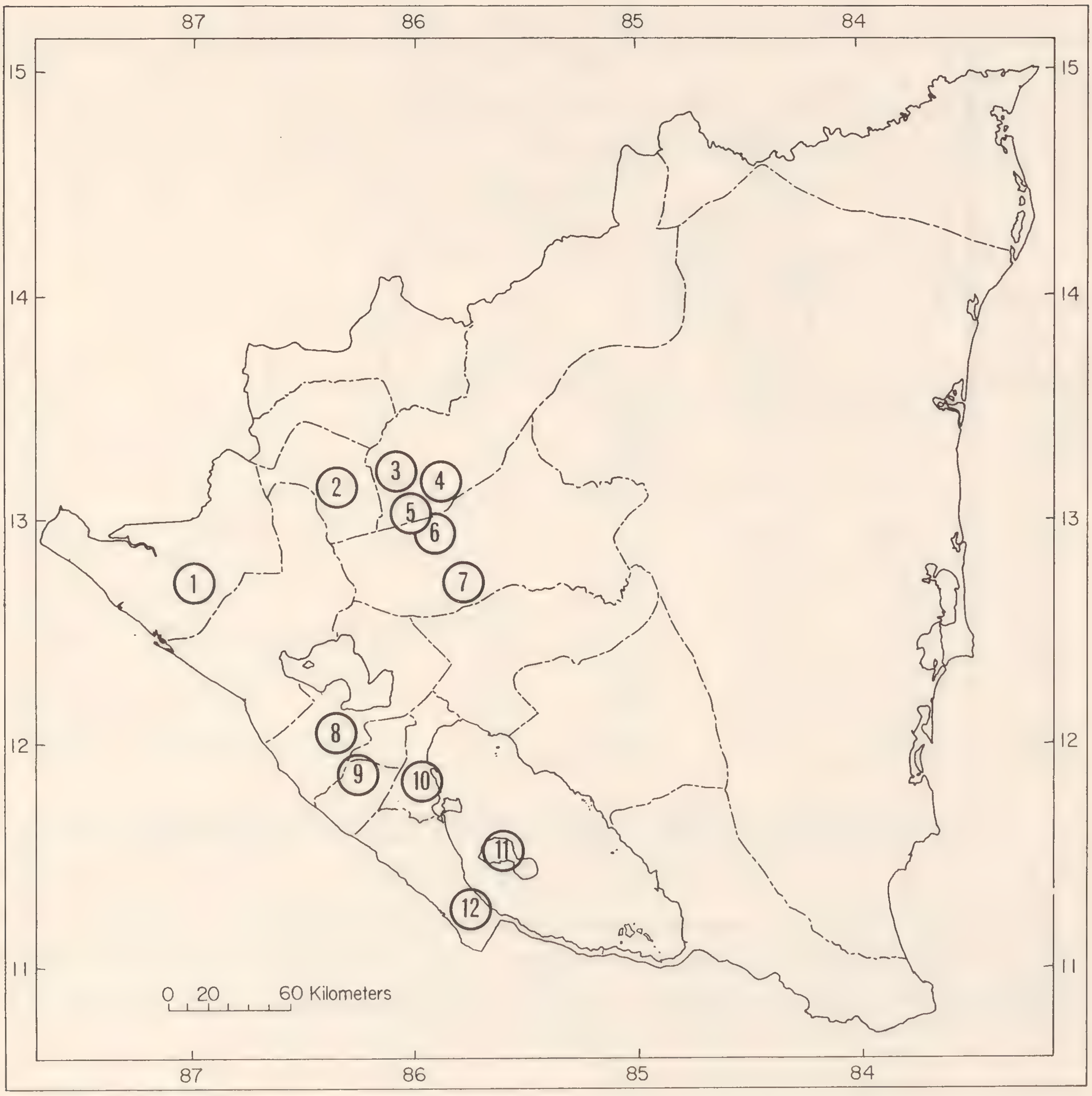

FIG. 1.—Geographic localities of samples included in multivariate analysis of populations of *P. gymnotis* and *P. mexicanus*: 1) Volcán Casita, Chinandega; 2) 9 mi. NNW Estelí, Estelí; 3) specimens labeled with reference to San Rafael del Norte, Jinotega; 4) Hda. la Trampa, Jinotega; 5) specimens labeled with reference to Jinotega, Jinotega; 6) Hda. Tepeyac and Santa María de Ostuma, Matagalpa; 7) specimens labeled with reference to Esquipulas, Matagalpa; 8) south-central Managua; 9) vicinity Diriamba, Carazo; 10) specimens labeled with reference to Guanacaste, Granada; 11) Isla de Ometepe, Rivas; 12) southern Rivas.

Measurements.—Average and extreme external measurements of 30 adults (17 males, 13 females) from southeast of Guanacaste, Granada, are: total length, 231.4 (217-254); length of tail, 115.8 (104-129); length of hind foot, 25.0 (24-26); length of ear, 20.5 (19-21). Males in this series averaged 42.8 (37.0-50.2) grams in weight and 11 nonpregnant females averaged 41.9 (31.4-46.7). Cranial measurements are given in Tables 1 and 3.

Remarks.—*P. gymnotis* is here reported for the first time from Nicaragua, where it evidently occurs the length of the western

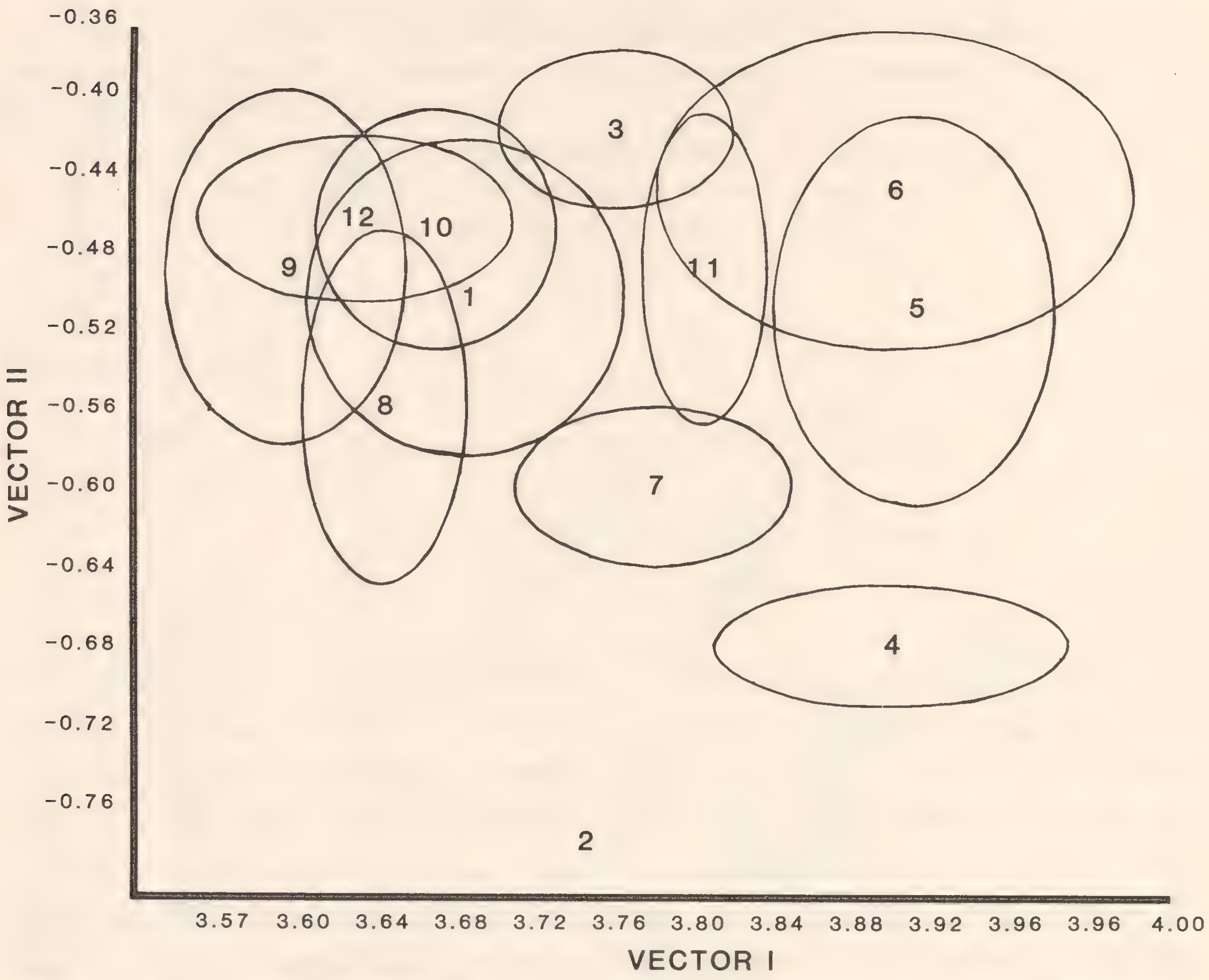

FIG. 2.—Projection of sample means (± one standard deviation) for the first two canonical variates in 12 samples of *Peromyscus* from Nicaragua. Numbers represent samples used to analyze geographic variation (see legend Fig. 1). The number lacking an ellipsis represents a sample containing only one specimen.

part of the country. Previously, this species was known only from southeastern Chiapas and southern Guatemala (Huckaby, 1980). The specimens reported here suggest that *gymnotis* also will be found in El Salvador, southern Honduras, and probably into northwestern Costa Rica.

P. gymnotis long was considered a subspecies of *P. mexicanus* and, as noted above, the relationships between the two remain somewhat uncertain. They differ mainly in size (*mexicanus* is the larger) and type of habitat. *P. gymnotis* occupies lowland habitats along the Pacific coast of Middle America from eastern Chiapas to southern Nicaragua. Where the range of *mexicanus* approaches that of *gymnotis*, the former is found at higher (inland) localities. The two species are not known to occur sympatrically in Nicaragua or elsewhere, and morphological intergradation between them has not been demonstrated (but see previous discussion).

P. gymnotis also differs from *mexicanus* in that few specimens have any degree of blotching on the underside of the tail as is

TABLE 2.—*Eigenvalues of selected canonical variates showing the percentage influence of each character in comparative measurements of* Peromyscus mexicanus *(seven samples) and* P. gymnotis *(five samples). Eigenvalues shown represent the normalized vector coefficient of each character. The median is a value in millimeters that reflects an approximate midpoint between the largest and smallest actual measurement of each character.*

		Vector I		Vector II	
Character	Median	Eigenvalue	Per cent influence	Eigenvalue	Per cent influence
Greatest length of skull	31.29	0.0408	22.20	0.0115	5.85
Interorbital breadth	4.98	−0.0434	3.76	−0.1781	14.37
Breadth of braincase	13.48	0.0790	18.55	−0.0571	6.17
Depth of braincase	10.21	0.0718	12.76	0.0151	2.50
Length of rostrum	12.41	0.0109	2.35	−0.0228	4.58
Length of palate	4.60	0.0386	3.09	0.1900	14.16
Length of maxillary toothrow	4.69	0.1737	14.19	0.3095	23.49
Length of incisive foramen	6.22	0.0853	9.23	−0.0540	5.44
Breadth of rostrum	5.50	−0.1423	13.63	−0.0802	7.15
Breadth of zygomatic plate	2.41	−0.0046	0.19	0.2548	9.95

common in populations of the latter. In more than 150 museum skins of *gymnotis* examined by us from Nicaragua, only 21 specimens had any blotching ventrally on the tail, and in most cases even this was minimal. Thus the tail of typical *gymnotis* is more or less unicolored in contrast to the typically heavily blotched tail in *mexicanus*.

We assume that *P. gymnotis* once was distributed throughout most of the dry deciduous forest and semievergreen rain forest that was typical of western Nicaragua but now has been mostly destroyed as a result of agricultural practices. The species evidently still occurs sparingly in riparian situations in this region where some forest remains, such as at San Antonio, Chinandega (see Genoways and Jones, 1972), and in the wooded areas bordering Lake Nicaragua in southern Rivas. It is abundant, however, on the forested sides of isolated volcanos (Volcán Casita and Volcán Mombacho in our collections, for example), and on the hills (Meseta de los Pueblas) to the south of Lake Managua. In such situations, mice typically were trapped in forest, some second growth, and along the wooded borders of cafetals, especially around fallen logs and the large roots of trees.

In our material there are pregnant females taken in the months of March, April, and June through August; lactating animals were obtained in April and August, and juveniles were trapped in March, June, July, and August. Sixteen gravid females carried an

TABLE 3.—*Cranial measurements of adults of three species of* Peromyscus *from Nicaragua.*

Specimens or samples	Greatest length of skull	Zygomatic breadth	Interorbital breadth	Breadth of braincase	Depth of braincase	Length of rostrum	Length of palate	Length of maxillary toothrow	Length of incisive foramen	Breadth of rostrum	Breadth of zygomatic plate
Peromyscus stirtoni											
KU 71541, ♀	29.7	13.8	5.0	13.2	10.5	11.0	4.5	4.2	5.3	5.0	2.4
KU 71542, ♂	29.5	14.2	5.2	13.7	10.2	11.6	4.4	4.3	5.4	5.4	2.4
KU 106797, ♀	28.5	12.9	4.9	12.8	9.3	12.1	4.3	3.9	4.9	4.6	2.6
KU 106798, ♀	30.2	13.8	4.7	12.6	9.7	12.0	4.6	4.2	5.8	5.0	2.4
KU 115570, ♂	30.3	14.3	5.0	13.1	9.9	11.9	4.3	4.3	5.9	5.1	2.7
KU 115571, ♀	28.9	14.0	5.0	12.9	10.2	11.1	4.6	4.2	5.5	5.0	2.4
KU 115572, ♂	29.7	14.2	4.8	13.1	10.0	11.5	4.6	4.2	5.8	5.0	2.3
Peromyscus gymnotis vicinity Guanacaste, Granada											
Sample size	30	20	30	30	29	28	30	30	30	30	30
Mean	31.1	15.2	5.0	13.3	10.0	12.3	4.5	4.7	6.2	5.5	2.3
Minimum	29.8	14.3	4.6	12.5	9.5	11.6	4.2	4.4	5.8	5.1	1.9
Maximum	32.5	16.2	5.3	14.0	10.5	13.3	4.9	5.0	6.7	6.0	2.6
1 SE	0.11	0.12	0.03	0.07	0.05	0.08	0.04	0.03	0.05	0.04	0.03
CV	2.0	3.4	3.4	2.8	2.8	3.2	4.7	3.4	4.5	4.3	6.2
Peromyscus mexicanus northern Matagalpa											
Sample size	33	24	37	37	37	30	37	37	37	37	37
Mean	32.5	15.6	5.0	13.9	10.5	12.9	4.8	4.9	6.5	5.5	2.5
Minimum	30.6	14.2	4.7	13.2	10.0	11.9	4.3	4.4	5.9	4.7	2.1
Maximum	34.8	16.6	5.4	14.8	11.4	14.0	5.5	5.4	7.1	6.0	2.9
1 SE	0.16	0.11	0.03	0.06	0.06	0.09	0.04	0.04	0.05	0.04	0.03
CV	2.8	3.5	3.3	2.8	3.3	3.8	5.0	4.9	4.3	4.7	7.5

average of 2.7 (2-4) fetuses (mode 3). Ranges of length of testes in adult males were: March, 15 (one animal); April, 13-18; June, 12-20; July, 12-18; August, 13-18. Maturational molt patterns on juveniles are typical of those described for other species of the genus.

Specimens examined (248).—CARAZO: *3 mi. NW Diriamba, ca. 660 m.*, 59 (71479-526, 71956-66); 3 km. N, 4 km. W Diriamba, 600 m., 54 (110541-63, 115531-61). CHINANDEGA: Hda. Bellavista, Volcán Casita, 720 m., 32 (106764-95); San Antonio, 35 m., 1 (106796). GRANADA: Finca Santa Cecilia, 6.5 km. SE Guanacaste, 660 m., 45 (106799-843); *Finca El Progreso, 10 km. SE Guanacaste, 1000 m.*, 10 (106844-53). MANAGUA: 3 mi. SE El Crucero, 2 (71478, 71543); *6 mi. WSW Managua*, 1 (71477); *13 km. S Managua*, 2 (104603-04). RIVAS: Hda. Amayo, 13 km. S, 14 km. E Rivas, 40 m., 6 (98088-93); *Río Javillo, 3 km. N, 4 km. W Sapoá, 40 m.*, 2 (106854-55).

Additional record.—CHINANDEGA: *Volcán de Chinandega* (Allen, 1908:659).

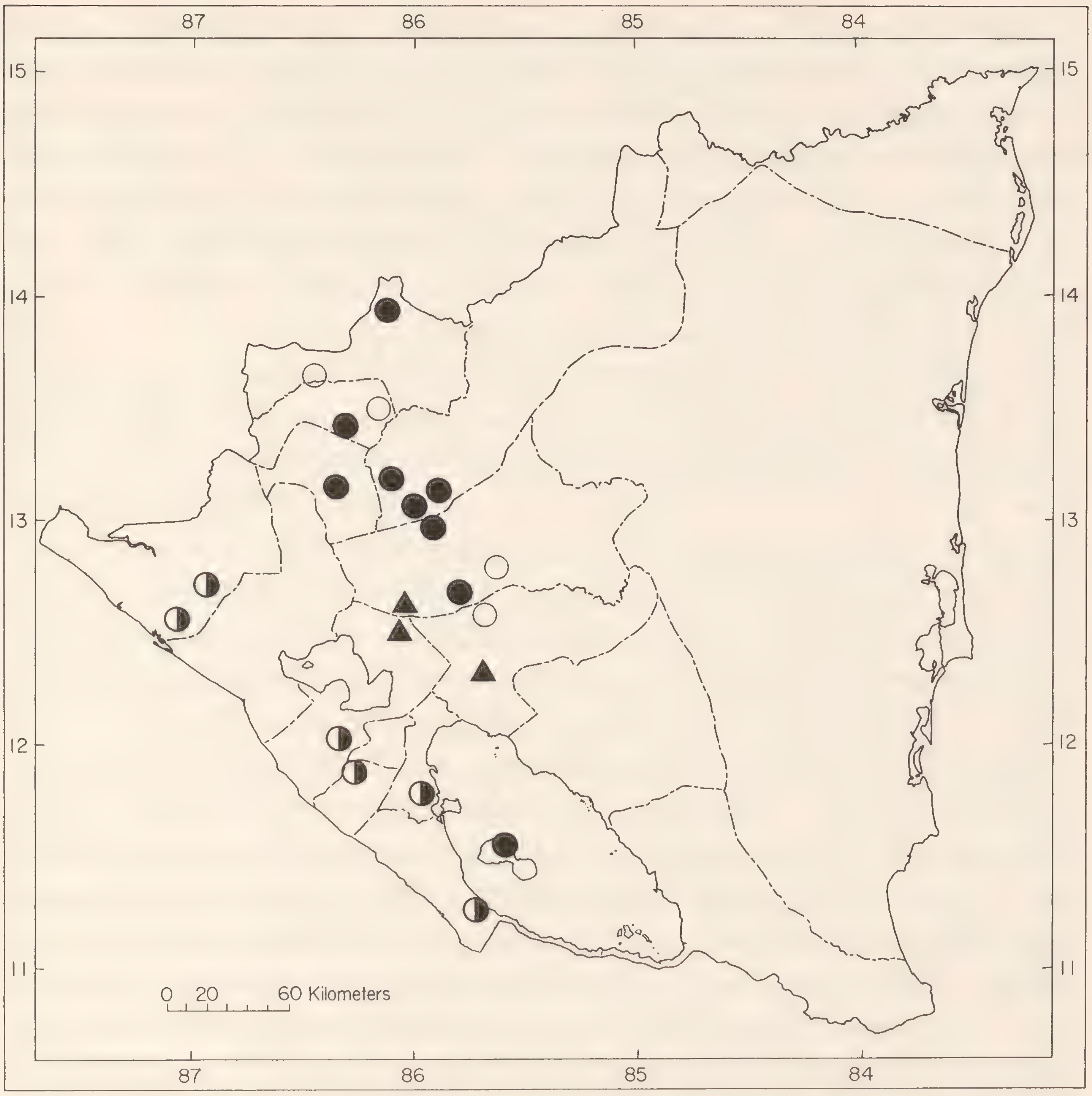

FIG. 3.—Distribution in Nicaragua of *Peromyscus gymnotis* (half solid circle), *P. mexicanus* (solid or open circle), and *P. stirtoni* (triangle). The open symbols represent records from the literature.

Peromyscus mexicanus saxatilis Merriam, 1898

Distribution in Nicaragua.—Forested areas of Cordillera Central and associated highlands probably south at least to northern Boaco; also on isolated volcanos of Isla de Ometepe in Lake Nicaragua (Fig. 3).

Measurements.—Average and extreme external measurements of 29 adults (16 males, 13 females) from Santa María de Ostuma, Matagalpa, are: total length, 251.2 (230-269); length of tail, 125.6 (112-143); length of hind foot, 25.7 (24-28); length of ear, 21.3 (18-23). Fourteen males in this series averaged 48.1 (38.9-55.1) grams in weight and eight nonpregnant females averaged 46.8 (40.0-51.5). See Table 3 for cranial measurements.

Remarks.—This mouse is a common inhabitant of wooded areas in the mountains of north-central Nicaragua, south at least to the southern part of Matagalpa and probably into northern Boaco. At Santa María de Ostuma, for example, *P. mexicanus* was abundant in cloud forest partially cleared for the planting of coffee. Specimens were taken there in traps set along logs and around stumps and the roots of living trees, most often in association with *Reithrodontomys brevirostris*.

Because *P. mexicanus* occurs in the mountains of Costa Rica and western Panamá, the species once may have been more or less continuously distributed from north to south through the area now known as the Nicaraguan Gap. Its presence on the volcanos of Isla de Ometepe, in Lake Nicaragua, may be a relictual reflection of this once broader distributional pattern. Little collecting has been done in southern Nicaragua to the east of the Lake, however, and it is possible that *mexicanus* is present on some of the few "highlands" (mostly low hills) in that area.

Some relationships between *P. mexicanus* and *P. gymnotis* are discussed in the account of the latter species. Mice from Isla de Ometepe are of interest in this context because their insular habitat is much nearer the known range of *gymnotis* in Nicaragua than that of *mexicanus*. Our specimens from Ometepe were taken on the lower slope of Volcán Concepción in a cafetal having a good canopy of mature trees and containing many fallen logs and some rocks. The individuals from Ometepe resemble *gymnotis* in that their tails lack the blotching characteristic of *mexicanus*. However, they have the large external dimensions typical of *mexicanus* and cluster with that species (Fig. 2) in cranial size. Moreover, all but one of eight specimens have a clearly divided anterocone on the first upper molar, a condition typically lacking in *gymnotis* (Huckaby, 1980) and in all specimens assigned by us to that taxon from the adjacent mainland of Rivas.

Juveniles in our sample are represented by mice taken in the months of January, March through July, November, and December. Pregnant females were obtained in March, April, June, and July; nine carried an average of 2.4 (1-4) fetuses. Lactating females are at hand from March, April, and July. Testes of adult males measured 10-16 in length in March, 15-17 in April, 15-17 in June, and 15 (three specimens) in July.

Some of J. A. Allen's (1908, 1910) localities where W. B. Richardson collected are difficult to find on modern maps. The one labeled as "Rio Coco" was discussed by Jones and Genoways

(1970). Another that is important to us, because *P. mexicanus* was listed from there, is "Chontales." Allen (1908:647) erroneously located this place in the "lowlands east of Lake Nicaragua, altitude about 500 to 1000 feet." Subsequently, he (1910:87-88) corrected the location of this site by listing it as on the "east slope of the highlands" and indicating that it actually was at an altitude of 1000 to 1500 feet and in the general vicinity of other localities in Matagalpa at which Richardson collected. Allen (p. 87) further corrected his earlier designation for "Chontales" by noting that Richardson made no collections in "the lowlands, including the borders of Lakes Managua and Nicaragua and the southern and coast regions below 500 feet."

We have been unable to locate any specific place bearing the name "Chontales" on Nicaraguan maps available to us. The modern departamento by that name is too far south to have been visited by Richardson. However, the present-day Departamento de Boaco, which borders Matagalpa on the south, was part of Chontales in the early 1900's when Richardson worked in Nicaragua. We think it likely that his locality "Chontales" was within the border of the old departamento by that name, just to the south of places in Matagalpa such as Uluse, Río Grande, and Muy Muy where he is known to have collected mammals. This would place it in the general vicinity of Tierra Azul, about 30 km. NNE Boaco and at the approximate coordinates of 12°41′N, 85°30′W.

Specimens examined (149).—Esteli: 9 mi. NNW Estelí, ca. 910 m., 1 (71424). Jinotega: 1 mi. NW San Rafael del Norte, 5 (71425-29); Hda. la Trampa (5.5 km. N, 16 km. E Jinotega, ca. 1100 m.), 10 (99490-99); *1 mi. NW Jinotega*, 1 (71430); 5 mi. S, 2 mi. E Jinotega, 15 (71431-46). Madriz: Daraili, 5 km. N, 14 km. E Condega, 490 m., 1 (98086). Matagalpa: Santa María de Ostuma, 1250 m., 53 (106733-63, 110525-40, 115498-503); *Hda. Tepeyac (10.5 km. N, 9 km. E Matagalpa), ca. 960 m.*, 23 (104602, 104605-26); 2 km. N, 6 km. E Esquipulas, 960 m., 22 (115504-25); *La Danta, 1 km. N, 5 km. E Esquipulas, 780 m.*, 6 (115526-30, 115633). Nueva Segovia: 1.5 km. N, 1 km. E Jalapa, 660 m., 4 (110521-24). Rivas: 2 km. N, 3 km. E Mérida, 200 m., Isla de Ometepe, 8 (115562-69).

Additional records (Allen, 1908:659, 1910:100).—Boaco: Chontales (see text). Jinotega: *Peña Blanca*; *San Rafael del Norte*. Madriz: Río Coco (see Jones and Genoways, 1970:8, 10). Matagalpa: *Matagalpa*; Uluse. Nueva Segovia: Ocotal.

Peromyscus stirtoni Dickey, 1928

Distribution in Nicaragua.—Known only from west-central part of country in departments of Boaco, Managua, and Matagalpa; probably occurring elsewhere in relatively low and dry interior habitats northward to Honduran-Salvadorian border (see Fig. 3).

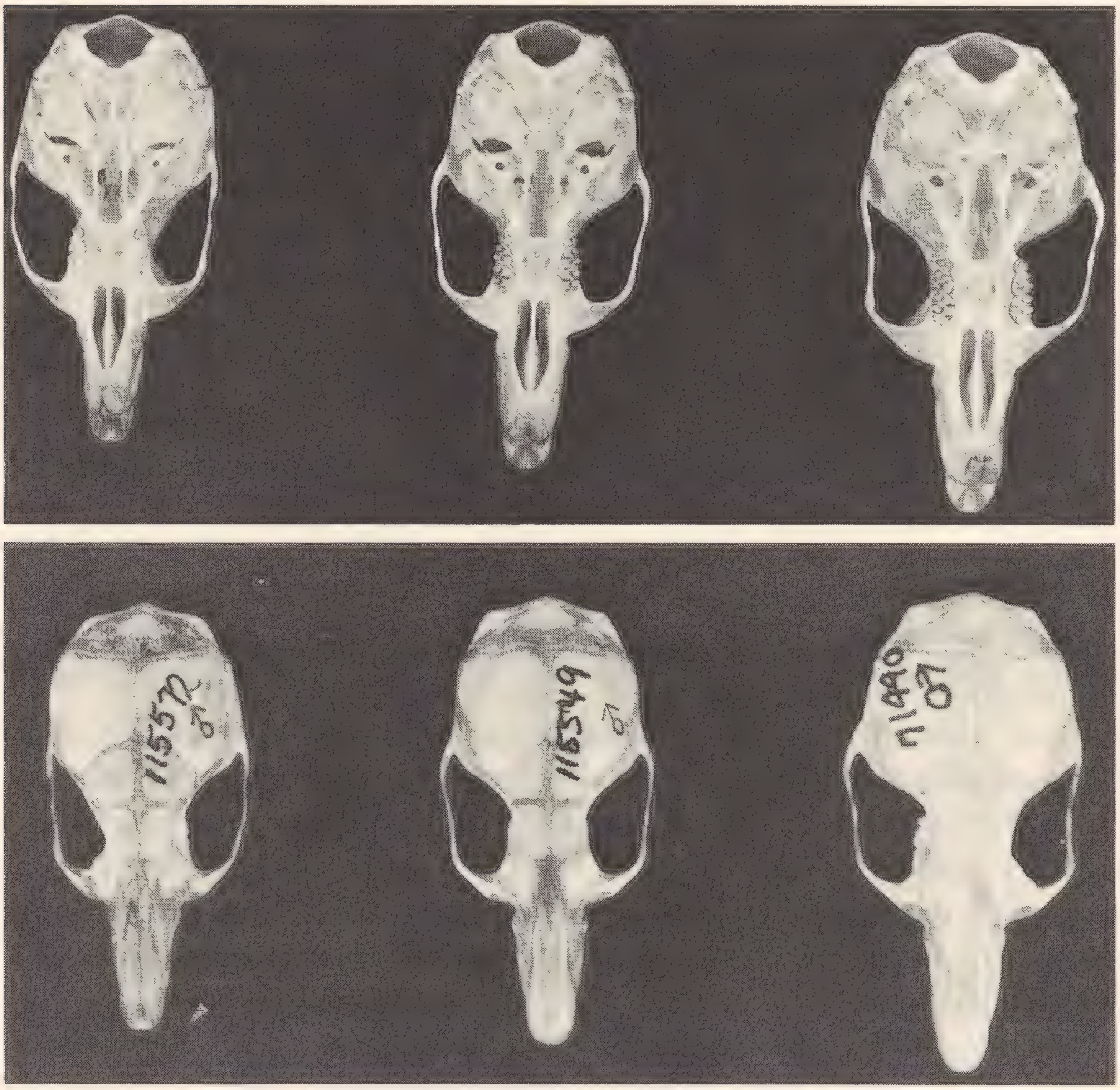

Fig. 4.—Dorsal and ventral views of typical skulls of *P. mexicanus* (KU 71440, ♂, left), *P. gymnotis* (KU 115549, ♂, center), and *P. stirtoni* (KU 115572, ♂, right).

Measurements.—External measurements of three males and three females, respectively, are: total length, 195, 200, 195, 191, 204, 207; length of tail, 96, 95, 86, 94, 95, 107; length of hind foot, 24, 23, 22, 23, 23, 22; length of ear, 19, 19, 18, 19, —, 21. Two males and a nonpregnant female weighed 31.3, 28.1, and 28.2 grams. Cranial measurements are given in Table 3.

Remarks.—This species has not been reported previously from Nicaragua, but is known from nearby localities in southern Honduras and eastern El Salvador (Huckaby, 1980). It is noticeably smaller than *P. gymnotis* and *P. mexicanus* (see Fig. 4 and Table 3) and differs also in having beaded supraorbital ridges, a well-haired and bicolored tail, and somewhat paler dorsal pelage. A buffy pectoral patch is moderately to well developed in five of the six museum skins we examined.

Specimens from Los Cocos were trapped in dry forest and brush adjacent to a rocky river bed. The two from north of Las Maderas were taken along a small rocky ridge above a steep slope that supported a weedy cornfield. Testes of two April-taken males measured 18 and 20 in length. A female captured on April 4 carried three fetuses measuring 24 in crown-rump length; one taken in March and two from August evinced no detectable reproductive activity.

Specimens examined (7).—Boaco: Los Cocos, 14 km. S Boaco, 220 m., 3 (115570-72). Managua: 8 km. (by road) N Las Maderas, 380 m., 2 (106797-98). Matagalpa: 11 km. SE Dario, 2 (71541-42).

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The present work was initiated to investigate further the preliminary electrophoretic findings of Straney *et al.* (1979) and Straney (1981) who suggested that the genus *Artibeus* is an artificial assemblage of species representing several evolutionary lineages within the subfamily Stenodermatinae. Specifically, we examined the phenetic and cladistic relationships among four species of small *Artibeus* (*A. cinereus, A. toltecus, A. phaeotis,* and *A. watsoni*) as compared to single individuals of the large species (*A. jamaicensis* and *A. concolor*) as indicated by protein electrophoresis. Specific questions addressed were as follows: What are the inter- and intraspecific relationships of these four small species? Did the smaller species share a common ancestry after divergence from the lineages of the larger *Artibeus jamaicensis* and *A. concolor*? Is the genus *Artibeus* a composite taxon resulting from combining species that have retained the exophenotypically primitive condition, as suggested by the studies of Straney *et al.* (1979) and Straney (1981)? The relationship between the small *Artibeus* and other congeneric species (*A. jamaicensis* and *A. concolor*) relative to representatives of *Chiroderma, Uroderma* and *Vampyrops* will be examined in an effort to determine the primitive condition.

Methods and Materials

Bats were collected with mistnets from natural populations. Immediately after sacrifice, liver, kidney, and heart samples were removed and frozen in liquid nitrogen. Methods for tissue preparation, starch gel electrophoresis, and enzyme designations were similar to those of Selander *et al.* (1971) as modified by Greenbaum and Baker (1976). Twenty-two isozymes (presumptive loci) consisting of enzymatic and nonenzymatic proteins were assayed. Lactate dehydrogenase -1 and -2 (Ldh-1, 2), Malate dehydrogenase -1,2 (Mdh-1,2), Isocitrate dehydrogenase -1,2 (Idh-1,2), Lactate dehydrogenase -1,2 (Ldh-1,2), Phosphoglucomutase -1,2 (Pgm-1,2), Hemoglobin (Hb), Indophenol oxidase -1,2 (Ipo-1,2), Glutamate oxalate transaminase -1,2 (Got-1,2), and Mannose-6-phosphate isomerase (Mpi) were resolved using a triscitrate pH 6.7 continuous buffer system. Albumin (Alb), Alcohol dehydrogenase (Adh), 6-Phosphogluconate dehydrogenase (6-Pgd), Phosphoglucose isomerase -1,2 (Pgi-1,2), and Peptidase -1,2,3 (Pep-1,2,3) were resolved using a triscitrate pH 8.0 continuous buffer system. The substrate used for resolving Pep-2 was the dipeptide Glycyl-L-leucine and for Pep-1 and -3, tripeptide Leucyl Glycyl glycine. Esterases were examined, but we were unable to score them confidently because of the high degree of variability among species and populations. To verify results, all individuals were electrophoresised at least twice for each system, and subsequent scoring was blind relative to previous scoring. This type of testing of results revealed consistent scoring.

To assess primitive and derived character states of the isozymes, *Artibeus jamaicensis, A. concolor, Uroderma bilobatum, Chiroderma villosum,* and *Vampyrops brachycephalus* were used as outgroups for *Artibeus cinereus, A. phaeotis, A. toltecus,* and *A. watsoni.* Plesiomorphic states were assigned on the basis of shared allozymes between one or more outgroups and one or more species within the group examined. After determining the primitive condition, we resolved autapomorphic and synapomorphic character states. A cladogram was then drawn from a locus by locus analysis (Patton *et al.*, 1981). Presumed synonomous isozymes and allozymes were determined using side-by-side comparisons.

Further analysis of the electrophoretic data was done using the Fitch and Margoliash (1967) method to construct phylogenetic trees from Rogers' distance values, and a phenogram based on the UPGMA option (Rohlf and Kishpaugh, 1974) was generated using Rogers' similarity values (Rogers, 1972).

Presumed loci are listed numerically with "1" indicating the most anodally migrating isozyme; more cathodal loci are given respectively larger numbers. Particular allozymes are designated such that "a" represents the fastest migrating band and "b," "c," etc., indicate respectively slower migrating bands.

Specimens examined—Artibeus cinereus: Population 1—Suriname, Nickerie, Kabalebo, 1♂; Suriname, Nickerie, Sipaliwini, 3♀♀, 2♂♂; Population 2—Grenada, St. George, 0.5 km. E Vendome, 1♂; Population 3—Venezuela, Bolívar, 8 km. S, 5 km. E El Manteco, 1♂; Venezuela, Bolívar, 18 km. E El Manteco, 1♀; Venezuela, Bolívar, 28 km. E El Palmar, 1♀; Population 4—Venezuela, Mérida, Mérida, near Hotel Río Prado, 2♀♀, 1♂; Population 5—Venezuela, Barinas, 8 km. by road SW Santa Barbara, 1♂; Populations 6 and 7—Suriname, Para, Zanderij, 4♀♀, 2♂♂. *Artibeus watsoni*: Population 1—Nicaragua, Zelaya, 3 km. NW Rama, 3♀♀, 7♂♂, Nicaragua, Zelaya, 4.5 km. NW Rama, 1♂. *Artibeus toltecus*: Population 1—Costa Rica, Puntarenas, 2.1 mi. S, 1.1 mi. E San Vito, Las Cruces Tropical Botanical Gardens, 1♂; Population 2—México, Sinaloa, 3 mi. E Rosario, 1♂; México, Chiapas, 23.6 mi. N Huixtla, 1♀. *Artibeus phaoetis*: Population 1—México, Sinaloa, 3 km. E Rosario, 1♂; Population 2—México, Nayarit, 0.4 mi. E of Hwy 15 to Acoponeta, 1♀, 1♂; Population 3—México, Guerrero, 24.1 mi. N Río La Union on Hwy 200, 4♀♀, 3♂♂; Nicaragua, Léon, 2.1 mi. SSE Léon on Nic 12, 2♀♀, 3♂♂; Population 4—México, Chiapas, 23.6 mi. N Huixtla, 1♀, 4♂♂; Population 5—Nicaragua, Zelaya, 4.5 km. NW Rama, 2♀♀, 3♂♂. *Artibeus concolor*: Suriname, Para, Zanderij, 1♂. *Artibeus jamaicensis*: Suriname, Commewijne, Niewuwe Grand Plantation, 1♂. *Chiroderma villosum:* Bolivia, Dept. La Pat, 1 mi. W Puerto Linares, 1♂. *Uroderma bilobatum*: Suriname, Brokopondo, Brownsberg Nature Park, 2 km. S Brownsberg, 1♀. *Vampyrops brachycephalus*: Venezuela, Monagas, Carapito, 1♀. All specimens from Suriname and Venezuela are housed in the Carnegie Museum of Natural History. Specimens from near Huixtla and Rama are deposited in either The Museum, Texas Tech University, or the Texas Cooperative Wildlife Collection, Texas A&M University; the remaining specimens are in The Museum, Texas Tech University.

RESULTS

Of the 22 isozymes examined, only one (Mdh-1) was monomorphic for all individuals. The remaining 21 variable loci, or allozymes, and their frequencies are listed in Table 1. From these data, the primitive state of each isozyme was determined using *Artibeus jamaicensis, A. concolor, Uroderma bilobatum, Vampyrops brachycephalus,* and *Chiroderma villosum* as outgroups. Primitive states were found for all loci except Pep-3. Cladistic analysis of the derived character states of each isozyme resulted in the cladogram depicted in Fig. 1, which shows *Artibeus cinereus, A. watsoni, A. toltecus,* and *A. phaeotis* tied together by three polymorphic synapomorphies [Mdh-2(a), Pep-1(c), and Pep-2(a)]. Interspecific relationships within the small *Artibeus* could not be determined because of either reversals or convergence of character states in Alb(d) and Hb(a). In Fig. 1, the solid line ties together *A. watsoni* and *A. toltecus,* and the broken line ties together *A. watsoni* and *A. phaeotis*. *Artibeus cinereus* has at least twice as many

TABLE 1.—*Electrophoretic data for species of* Artibeus *and outgroups. See* Methods and Materials *section for explanation of isozyme and allozyme designations. If a locus is polymorphic for a given population, the allozyme frequencies are given in parentheses.*

	N	Mdh-2	Idh-1	Idh-2	Ldh-1	Ldh-2	Pgi-1	Pgi-2	Pgm-1	Pgm-2	Mpi	Pep-1	Pep-2	Pep-3	6-Pgdh	Alb	Hb	Got-1	Got-2	Adh	Ipo-1	Ipo-2
Artibeus cinereus																						
1	6	a(.17) b(.83)	b	b	a	a	b	b	b	b	b(.17) c(.83)	c(.67) d(.33)	b	c	b	e	c	b	c	c	a	a
2	1	b	b	b	a	a	b	b	b	b	b	c	b	c	b	e	c	b	c	c	a	a
3	3	a(.67) b(.33)	a(.33) b(.67)	a(.67) b(.33)	a	a	b	b	b	b	b(.67) c(.33)	b(.33) c(.33) d(.33)	b(.67) d(.33)	c	b	e(.67) d(.33)	c	b	c	c	a(.33) b(.67)	a
4	3	b	b	b	a	a	b	b	b	b	b(.17) c(.83)	d	a(.17) b(.83)	c	b	d	c	b	c	c	a	a
5	1	b	b	b	a	a	c	b	b	b	b(.50) c(.50)	d	b	c	b	d	d	b	c	c	a	a
6	3	b	a(.17) b(.83)	a	a	a	b	b	b	b	b(.17) c(.83)	d	a(.17) b(.83)	c	b(.67) c(.33)	d(.17) e(.67) f(.17)	b(.33) c(.33) d(.33)	b	c	c	a	a
7	3	a(.67) b(.33)	b	a(.67) b(.33)	a	a	b	b	b	b	b(.67) c(.33)	d	b	c	b	e	c(.67) d(.33)	b	c	c	a(.67) b(.33)	a
Artibeus watsoni																						
1	12	a(.73) b(.27)	b	b	a	a	a	b	b	b	c	c	a(.04) b(.94)	c	b	c	a(.18) b(.82)	b	c	c	a	a
Artibeus toltecus																						
1	1	a	b	b	a	a	b	b	b	b	c	c	a(.50) b(.50)	c	b	b	a	b	c	b	a	a
2	3	a	b	b	a	a	b	a(.33) b(.67)	b	b	c	c	a(.17) b(.83)	c	b	b	a	b	c	b	a	a

TABLE 1.—*Continued.*

Artibeus phaeotis																						
1	1	a	b	b	a	a	b	b	a	b	c	c	b	c	b	d	d	b	c	c	b	a
2	2	a	b	b	a	a	b	b	a	b	a(.25) b(.50) c(.25)	c	b	c	b	d	d	b	c	c	b	a
3	7	a	a(.21) b(.79)	b	a	a	b	b	a	b	a(.07) b(.64) c(.29)	c	a(.07) b(.93)	c	b	d	d	b	c	c	b	a
4	5	a	b(.90) c(.10)	b	a	a	b	b	a	b	b(.90) c(.10)	c	a(.10) b(.90)	c	b	d	d	b	c	c	a(.40) b(.60)	a
5	8	a	a(.13) b(.74) c(.13)	b	a	a	b	b	a	b	b(.25) c(.69) d(.06)	c	b	c	b	c(.13) d(.87)	d	b	c	c	a(.62) b(.38)	a
Artibeus concolor	1	b	b	b	a	a	b	b	b	a	b	a	b	a	a	e	b	a	c	e	a	c
Artibeus jamaicensis	1	b	a	b	a	a	b	b	b	c	b(.50) c(.50)	b	b	a	b	d(.50) e(.50)	c	a	a	c	b	a
Vampyrops brachycephalus	1	b	c	b	a	a	d	b	a	b	b(.50) c(.50)	c	c	b	b	d	c	b	c	b	a	a
Chiroderma villosum	1	b	b	c	b	a	b	b	b	c	c	a	f	b	b	a(.50) b(.50)	d	a	c	a	b	b
Uroderma bilobatum	1	b	b	c	a	b	b	b	a	c	d	a	e	b	b	a	d	b	b	d	b	a

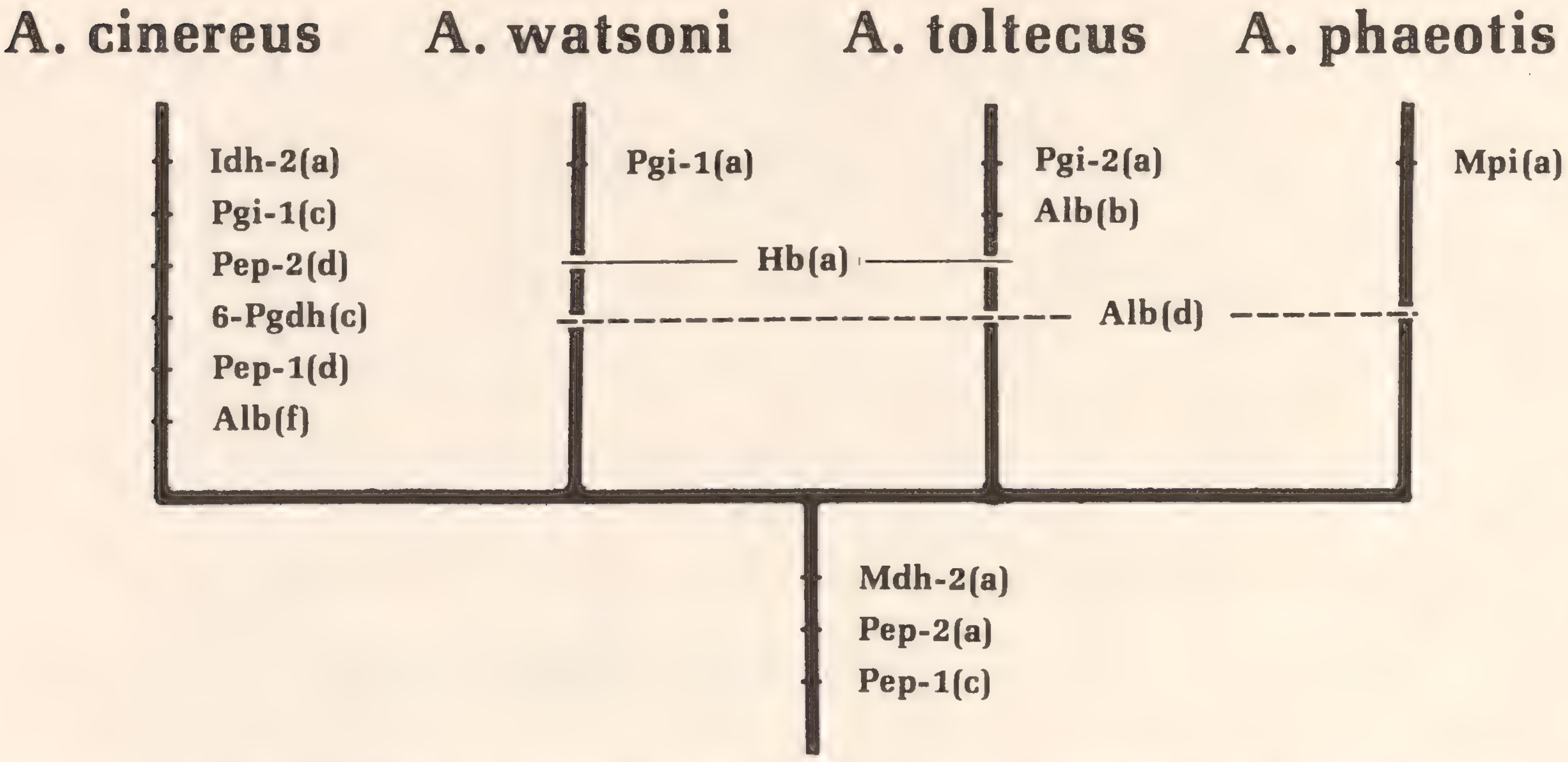

FIG. 1.—A cladogram based on shared derived electrophoretic characters of the small-sized species of *Artibeus*.

unique derived allozymes (6) as any of the other three small species of *Artibeus* examined. However, only *A. watsoni* is characterized by a fixed difference [Pgi-1(a)]. Indeed, the lack of fixed differences in the small species of *Artibeus* is very conspicuous.

In Table 2, polymorphism values, heterozygosity values, number of specimens examined, and number of fixed differences distinguishing a species from its congeners are presented along with results from other studies of species of phyllostomid bats. All calculations exclude values derived from esterases (Straney, 1981).

Clustering analysis based on Rogers' similarity values (Table 3) resulted in a distinct group representing the four species of small *Artibeus* examined in this study. The outgroups, each of which was represented by only a single individual, were significantly separate from the smaller species of *Artibeus* studied. The cophenetic correlation coefficient was 0.924. The maximum distance among the small *Artibeus* was 0.05 and the minimum distance to their nearest neighbor was 0.16 (Fig. 2).

Phylogenetic analysis using the Fitch and Margoliash method (1967) and Rogers' distance value (Rogers, 1972) resulted in two phylogenetic trees having the lowest F value (Prager and Wilson, 1978) and positive branch links (Fig. 3). The relationships among the small *Artibeus* were consistent in both phylogenetic trees. Only the position of *Artibeus concolor* and *A. jamaicensis* varied.

DISCUSSION

Perhaps the most startling aspect of the *Artibeus* data set is the low number of fixed allozymic differences that characterize *Arti-*

TABLE 2.—*Polymorphism, heterozygosity, fixed difference values, and references for various species within the family Phyllostomidae. The asterisk (*) denotes fixed differences relative to the genus* Artibeus. *All values presented exclude esterase variation.*

Species	Number examined	Polymorphism P (%)	Heterozygosity H	No. of fixed differences	Reference
Tonatia silvicola	6	16		3	Arnold, 1981
T. bidens	5	16		11	" "
T. carrikeri	1	5		4	" "
T. brasiliense	1	0		1	" "
T. schultzi	1	0		5	" "
T. nicaraguae	1	5		4	" "
T. venezuelae	1	10		7	" "
Micronycteris megalotis	3	16		4	" "
M. daviesi	1	0		3	" "
M. nicefori	6	30		5	" "
M. sylvestris	2	16		3	" "
M. minuta	5	40		10	" "
M. hirsuta	3	20		2	" "
M. schmidtorum	1	0		1	" "
M. brachyotis	1	0		6	" "
Monophyllus redmani	25	17		3	Baker et al., 1981
M. plethodon	10	8		3	" "
Macrotus waterhousii	118	10	.026	5	Greenbaum et al., 1976
M. californicus	100	14	.033	5	" "
Carollia perspicillata	57	24	.037		Straney et al., 1979
Anoura geoffroyi	30	17	.016		" "
Glossophaga soricina	19	6	.018		" "
Artibeus jamaicensis	48	24	.080		" "
A. jamaicensis	1	9	.090	1	This paper
A. concolor	1	0	.000	4	" "
A. cincereus	20	45	.023	0	" "
A. watsoni	12	14	.003	1	" "
A. toltecus	3	14	.030	0	" "
A. phaeotis	23	23	.035	0	" "
Vampyrops brachycephalus	1	5	.045	2*	" "
Chiroderma villosum	1	5	.045	5*	" "
Uroderma bilobatum	1	0	.000	4*	" "

beus cinereus, A. watsoni, A. toltecus, and *A. phaeotis.* Of these four species, only *A. watsoni* has a fixed unique allele [Pgi-1(a)], despite polymorphism levels that equal or exceed those of other phyllostomid species (Straney *et al.*, 1979; Greenbaum and Baker, 1976; calculated from Arnold, 1981). Except for *A. watsoni*, heterozygosity levels are only slightly less then the averages of other phyllostomid species ($P = 0.14$, $\bar{H} = 0.032$, Straney *et al.*, 1979). In comparable data sets from the same family, fixed differences among seven species of *Tonatia* averaged five (of 20 loci) per species. Among eight species of *Micronycteris*, fixed differences averaged 4.25 (of 21 loci) per species (Arnold, 1981), and in two sibling species of *Monophyllus* there were three (of 12 loci) (Baker *et al.*, 1981). The average number of fixed differences among *Artibeus cinereus, A. watsoni, A. toltecus,* and *A. phaeotis* was 0.25 (of

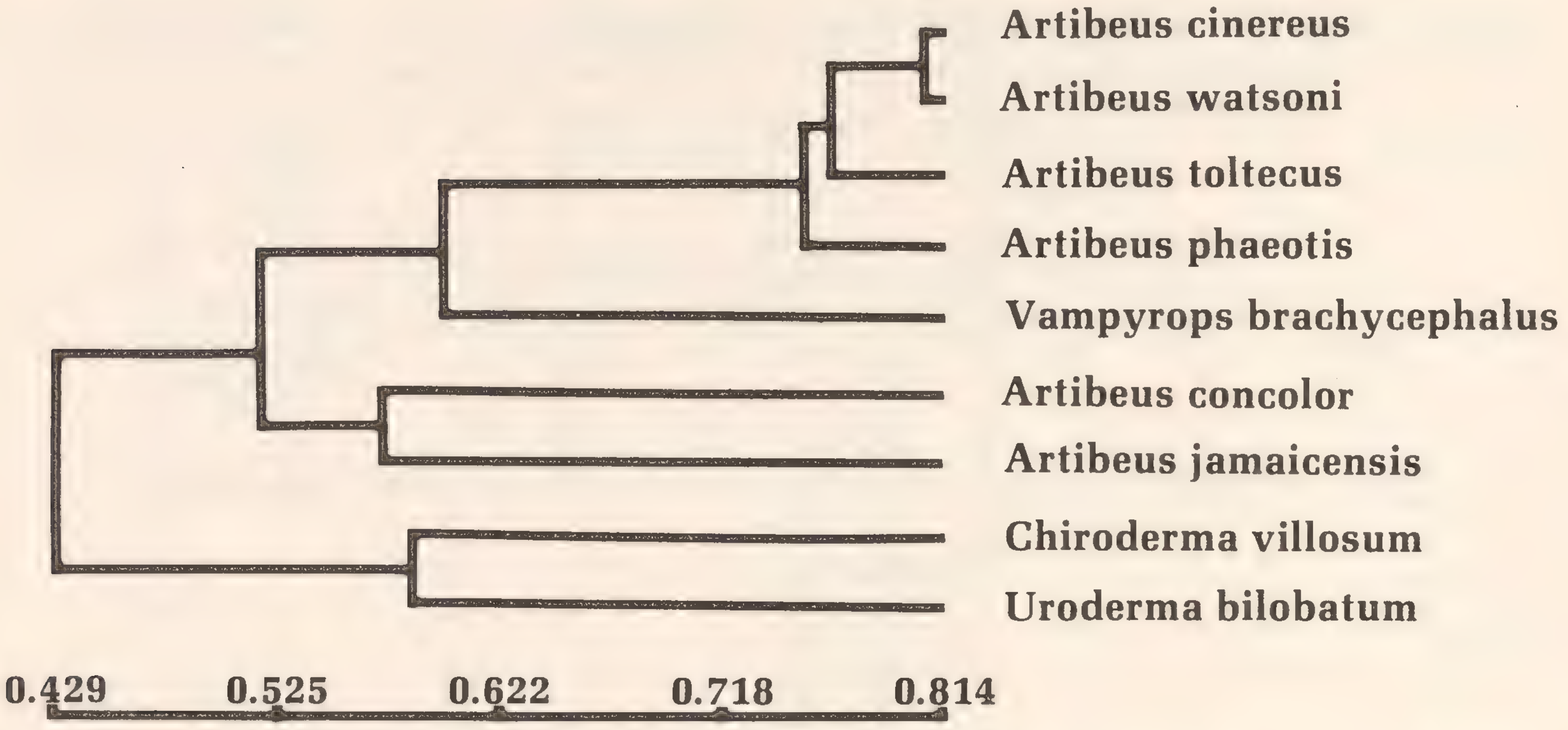

FIG. 2.—A phenogram of *Artibeus* species and outgroup taxa based on Rogers' similarity values.

22 loci). If genic evolution is progressing in a clocklike fashion in *Artibeus, Tonatia, Micronycteris,* and *Monophyllus,* then the divergence of *Artibeus cinereus, A. watsoni, A. toltecus,* and *A. phaeotis* was extremely recent relative to the speciation events in *Tonatia* and *Micronycteris*. Calculation of time since divergence based on fixed allozymic differences would suggest that either *Artibeus cinereus, A. watsoni, A. toltecus,* and *A. phaeotis* have only just diverged because they have even fewer fixed differences than sibling species of *Monophyllus* or perhaps because they are incipient species. If time since divergence was based on genetic similarity or distance (which uses polymorphic systems in measuring evolutionary distance), then the average age of species within the genera *Tonatia* and *Micronycteris (Nei's* I = 0.34 and 0.28, respectively, Arnold, 1981) would be greater than the average age of the small *Artibeus* (Rogers' S = 0.77). However, each of these small *Artibeus* species would then be older than the sibling species *Monophyllus redmani* and *M. plethodon* (Rogers' S = 0.83, Baker *et al.*, 1981), indicating that the number of fixed differences between congeners is not in all cases correlated with genetic distance, polymorphism, or heterozygosity. Species of *Tonatia, Micronycteris,* and *Monophyllus* all exhibit normal polymorphism levels and extensive allelic fixation. The small species of *Artibeus* do not exhibit extensive allelic fixation and exhibit higher than average polymorphism levels, particularly *Artibeus cinereus*.

Basing their hypothesis on electrophoretic analysis of several species within the family Phyllostomidae, Straney *et al.* (1979) suggested that *Artibeus* was a basal taxon for the rest of the sub-

TABLE 3.—*Rogers' genetic similarity and distance coefficients for species of* Artibeus *and outgroup taxa. Above the diagonal line are Rogers'* S *values and below the line are Rogers'* D *values.*

		1	2	3	4	5	6	7	8	9
Artibeus cinereus	1	—	.81	.75	.78	.56	.49	.64	.45	.66
Artibeus watsoni	2	.19	—	.80	.76	.52	.41	.56	.36	.52
Artibeus toltecus	3	.25	.20	—	.75	.50	.45	.58	.38	.48
Artibeus phaeotis	4	.22	.24	.25	—	.46	.44	.62	.51	.57
Artibeus concolor	5	.44	.48	.50	.54	—	.48	.41	.35	.57
Chiroderma villosum	6	.51	.59	.55	.56	.52	—	.38	.59	.51
Vampyrops brachycephalus	7	.36	.44	.42	.38	.59	.62	—	.44	.54
Uroderma bilobatum	8	.55	.64	.62	.49	.65	.41	.56	—	.45
Artibeus jamaicensis	9	.34	.48	.52	.43	.43	.49	.46	.55	—

family Stenodermatinae and that it represented a paraphyletic taxon. Further cladistic analysis based on a transformation series of the same data set (Straney, 1981) corroborated this hypothesis. Chromosomal data comparing species within the subfamily Stenodermatinae indicated that *Artibeus* has a conserved primitive karyotype (Baker *et al.*, 1979; Johnson, 1979). It is also important to note that between the small *Artibeus* examined and *Artibeus jamaicensis* there was only one fixed allozymic difference. Straney *et al.* (1979) also reported a high heterozygosity level (H = 0.08) in *Artibeus jamaicensis.* It is surprising to see so few fixed differences between *Artibeus jamaicensis* and *A. cinereus, A. watsoni, A. toltecus,* and *A. phaeotis,* despite a substantial genetic distance among them (Rogers' D = 0.24). A possible explanation is that *Artibeus* represents a basal taxon retaining primitive exophenotypic conditions and that the genus is a composite or paraphyletic taxon. If this proposal is correct and the genus is old relative to other genera in the family and subfamily—and if genic evolution behaves in a clocklike fashion—then one would predict that the genic distance among the species of *Artibeus* would be relatively large. As noted above, the genic divergence for the small species of *Artibeus* examined here is generally lower than in other genera of the Phyllostomidae. Thus, small species of *Artibeus* do not appear to be paraphyletic.

Systematically, the electrophoretic data indicate a close similarity among *A. cinereus, A. watsoni, A. toltecus,* and *A. phaeotis,* implying that these four species once shared a common ancestor after diverging from *A. jamaicensis, A. concolor, Chiroderma villosum, Vampyrops brachycephalus,* and *Uroderma bilobatum.*

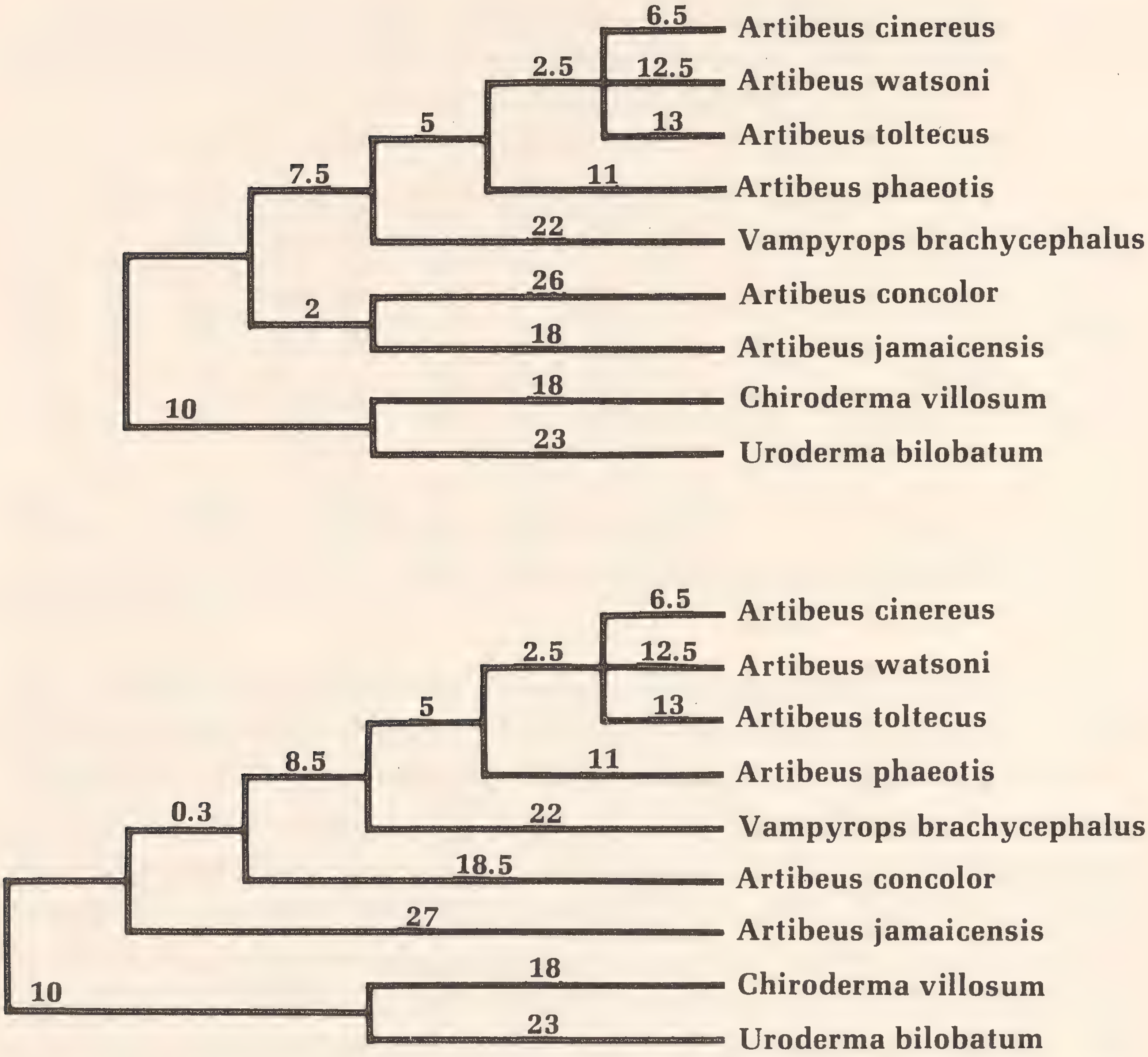

FIG. 3.—Fitch-Margoliash phylogenetic trees of *Artibeus* species and outgroup taxa. The F value for both trees is 6.4.

The common ancestry of these four species is documented by three polymorphic synapomorphies—Mdh-1(a), Pep-1(c), and Pep-2(a). However, the electrophoretic data do not document a common ancestry for the larger (*Artibeus jamaicensis* and *A. concolor*) and smaller (*A. cinereus, A. watsoni, A. toltecus*, and *A. phaeotis*) species of the genus *Artibeus* to the exclusion of the genus *Vampyrops*. If these electrophoretic data were used to define the systematics of the taxa examined, then either the genus *Artibeus* would include *Vampyrops brachycephalus*, or, within the currently recognized genus *Artibeus*, there would be at least two sister lineages to the genus *Vampyrops*. This is consistent with views suggesting that *Artibeus* is a paraphyletic taxon maintaining primitive exophenotypic conditions. Certainly the lack of fixed differences between the small *Artibeus* and *Artibeus jamaicensis* does not refute this stance.

Any attempt to analyze population differences electrophoretically, particularly in the widespread *Artibeus cinereus*, must rely solely upon polymorphic differences. For this type of study, large sample sizes are necessary from each population. Although not the purpose of the present study, it is interesting to note that populations 6 and 7 (Table 1), collected at the same locality, differed in seven of the nine polymorphic loci found at that location. The two populations were separated on the basis of ear color. Though the sample size is too small to draw conclusions, in a genus where species are differentiated electrophoretically on the basis of polymorphic differences, these figures represent a substantial difference. Larger sample sizes are needed to determine if there is a difference between these two groups.

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CRANIAL VARIATION AMONG POPULATIONS OF THE BLACK-TAILED PRAIRIE DOG IN NEW MEXICO

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Taxonomic relationships among populations have classically been derived from comparisions of skeletal morphology (Hall and Kelson, 1959; Sneath and Sokal, 1973). Populations of the same species that are similar in their morphometric traits and located close together geographically are usually considered to be genetically similar and, thus, comprise a uniform subspecies. Many studies have shown that geographically contiguous populations are similar in their skeletal dimensions (e.g., Kennedy and Schnell, 1978). However, studies examining species with patchy distributions have shown that phenetic relationships among populations may not exhibit geographic patterns, thereby making taxonomic classifications difficult (Berry *et al.*, 1978; Choate and Williams, 1978).

Populations of the black-tailed prairie dog, *Cynomys ludovicianus*, are widely separated from one another throughout their range from Canada to northern Mexico (Hall and Kelson, 1959). In the nineteenth century the distribution of prairie dogs was more or less continuous and their numbers were estimated at five billion (Seton, 1929). However, because of its alleged direct competition with livestock for forage and with agriculture for potential croplands, the prairie dog has been subject to attempted eradication by federal, state, and private interests (Koford, 1958; Smith, 1958; Cottam and Caroline, 1965; Madson, 1968). The distribution of prairie dogs has been reduced to relatively few scattered and somewhat isolated remnant populations. Reduction in potential genetic exchange among populations of prairie dogs increases the probability of differentiation by genetic drift and founder effect (Mayr, 1963). Isolation by distance may have especially profound effects on the prairie dog due to its sedentary nature (King, 1955).

Hansen (1977) concluded that the morphology of prairie dogs from the Tularosa Basin in New Mexico was sufficiently different from that of prairie dogs from other regions to merit subspecific status (no subspecific name was proposed) for the animals from the Tularosa Basin. Because prairie dogs were rare in that region, he classified them as endangered, a status currently recognized by the New Mexico Department of Game and Fish. However, this author (Chesser, 1981) found that genetic heterogeneity among populations of prairie dogs in New Mexico was high even when compared over relatively short geographic distances. Genetic findings do not support previous taxonomic classifications of this species, and amount of differentiation among local populations is often greater than that among populations from widely spaced physiographic regions.

Classifications derived from analyses of morphology and electrophoretic data often do not correspond (Schnell *et al.*, 1978; Schnell and Selander, 1981). Therefore, the discrepancies between the results of previous studies (Hansen, 1977; Chesser, 1981) could be an artifact of the type of data used. Studies which concentrate on differences over large geographic distances may essentially ignore the possibility of heterogeneity over limited space. Such studies do not take into consideration isolation of prairie dog populations by man-caused and natural factors which may enhance heterogeneity over short distances. My purpose in this study was to examine the variation of cranial dimensions of black-tailed prairie dogs from populations separated by short and long geographic distances in New Mexico. Statistical methods were employed to investigate whether classical methods of classification are appropriate for species with disjunct patterns of distribution.

MATERIALS AND METHODS

A total of 17 skull measurements were recorded from 318 adult black-tailed prairie dogs (188 males, 130 females) collected from 18 localities in New Mexico (Fig. 1A; Table 1). Localities were designated (Chesser, 1981) according to four regions separated by major geological formations: (1) the Clayton region, north of the bluffs of the Llano Estacado; (2) the Roosevelt County region, on

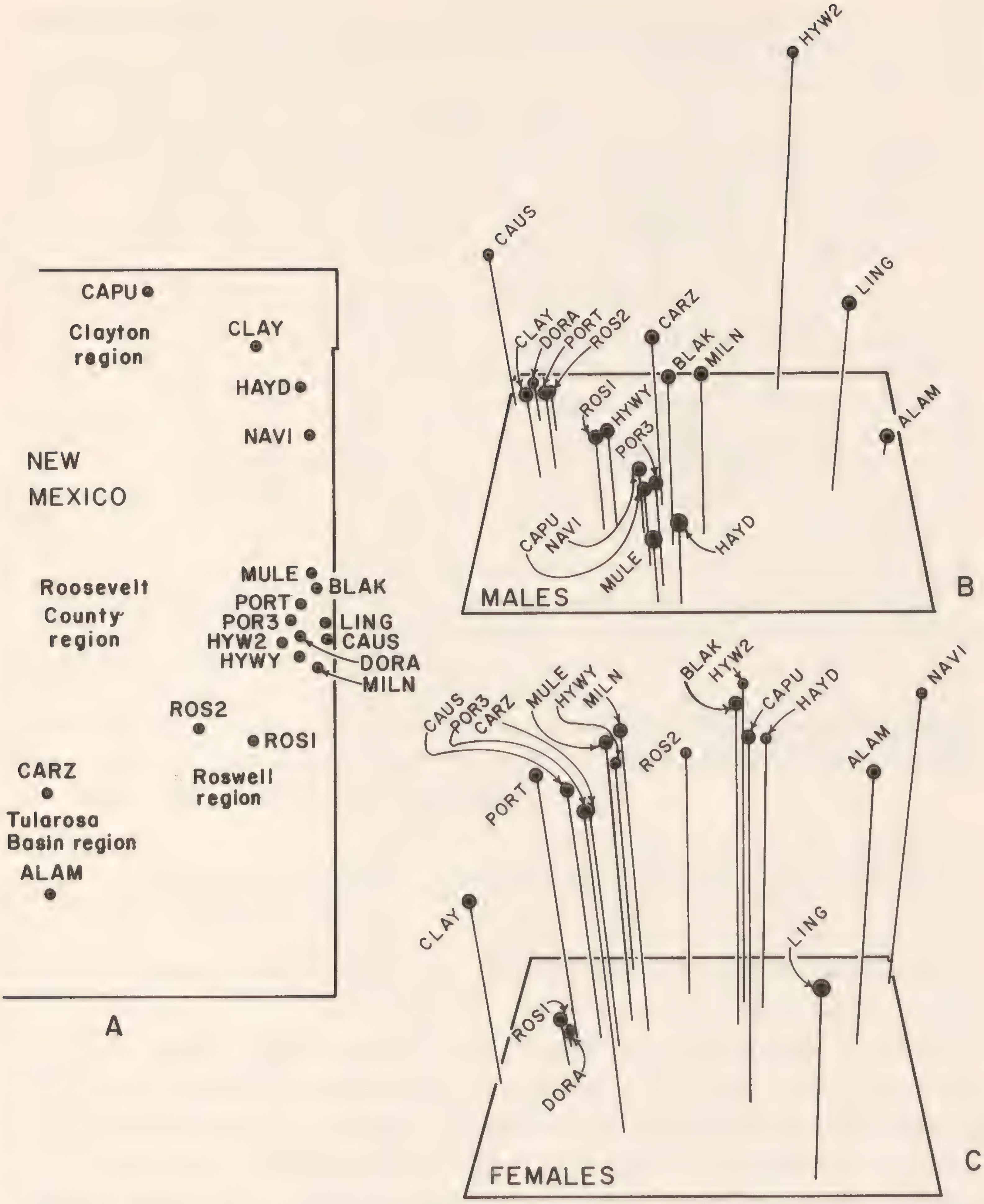

FIG. 1.—Map of collecting localities for black-tailed prairie dogs in New Mexico (A), and three-dimensional models depicting relationships among samples for male (B) and female (C) prairie dogs. The models were derived by principal components analysis using 17 cranial characters.

the Llano Estacado; (3) the Roswell region, on the premontane alluvial plain; and (4) the Tularosa Basin region, situated to the west of the Capitan Mountains. Prairie dogs from regions (1) and (2) are presently classified as *C. l. ludovicianus* (Hall and Kelson, 1959) whereas those from region (3) are *C. l. arizonensis* (Hall and Kelson, 1959) and those from region (4) represent the unnamed

TABLE 1.—*Collection localities of black-tailed prairie dogs in New Mexico. Sample abbreviations and regions refer to those depicted in Fig. 1A.*

Clayton Region

1. CAPU—8.5 km. NE Des Moines, Union Co., $n = 29$.
2. CLAY—12.8 km. S Clayton, Union Co., $n = 11$.
3. HAYD—9.6 km. E Hayden, Union Co., $n = 31$.
4. NAVI—10.7 km. SE Nara Visa, Quay Co., $n = 9$.

Roosevelt County Region

5. MULE—17.4 km. NE Portales, Roosevelt Co., $n = 7$.
6. BLAK—18.2 km. NE Portales, Roosevelt Co., $n = 14$.
7. PORT—9.5 km. E Portales, Roosevelt Co., $n = 78$.
8. POR3—19.1 km. S Portales, Roosevelt Co., $n = 9$.
9. CAUS—6.5 km. N Causey, Roosevelt Co., $n = 6$.
10. LING—2.0 km. SW Lingo, Roosevelt Co., $n = 5$.
11. DORA—3.5 km. W Dora, Roosevelt Co., $n = 11$.
12. HYW2—4.2 km. NW Hyway, Roosevelt Co., $n = 7$.
13. HYWY—1.0 km. E Hyway, Roosevelt Co., $n = 12$.
14. MILN—28.0 km. E Milnesand, Roosevelt Co., $n = 28$.

Roswell Region

15. ROS1—46.0 km. ENE Roswell, Chevas Co., $n = 7$.
16. ROS2—32.0 km. NNE Roswell, Chevas Co., $n = 9$.

Tularosa Basin Region

17. CARZ—31.0 km. W Carizozo, Lincoln Co., $n = 22$.
18. ALAM—17.5 km. NE Orogrande, Otero Co., $n = 21$.

endangered species (Hansen, 1977; previously designated *C. l. a.*, Hall and Kelson, 1959).

Cranial measurements (Fig. 2) were taken with dial calipers to the nearest 0.1 mm. as follows: (1) greatest skull length, (2) basal length, (3) rostral length, (4) nasal length, (5) upper diastemal length, (6) toothrow length, (7) premolar width, (8) third molar width, (9) rostral width, (10) palatine width, (11) post-palatal length, (12) length of auditory bulla, (13) width of auditory bulla, (14) greatest skull width, (15) mastoid breadth, (16) least interorbital width, and (17) greatest skull depth. Whenever possible, skull measurements were taken from the right side of the skull. Only adult prairie dogs with fully ossified skulls and completely closed cranial sutures were used in this study. This procedure reduced the variation in cranial dimensions attributable to animals of different ages since black-tailed prairie dogs appear to have determinant growth (King, 1955).

Univariate and multivariate statistics were used to analyze interlocality differentiation and sexual dimorphism of cranial dimen-

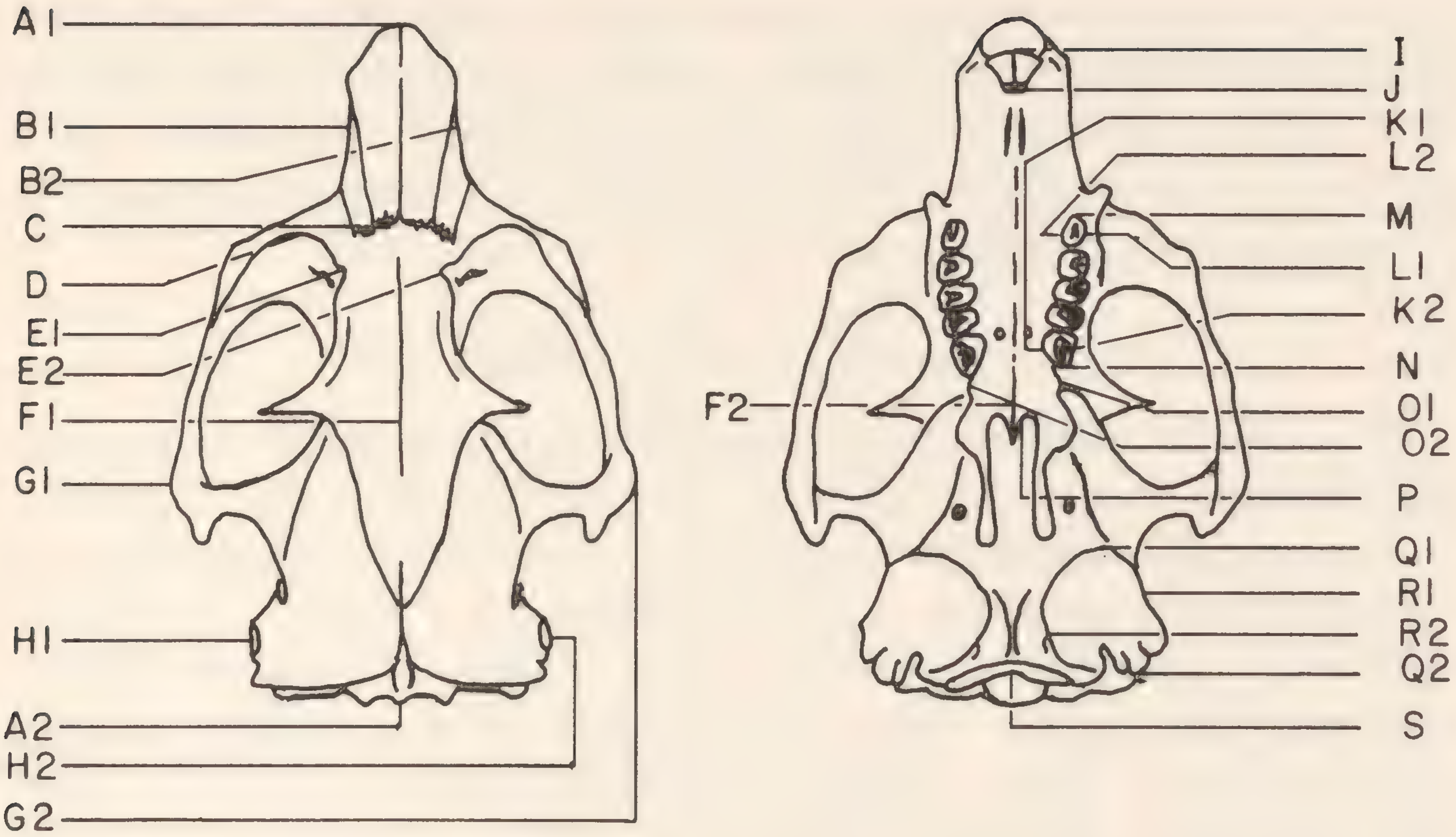

FIG. 2.—Skull measurements taken on adult black-tailed prairie dogs were as follows: greatest length (A1-A2); basalar length (I-S); rostral length (A1-D); nasal length (A1-C); diastemal length (J-M); maxillary toothrow length (M-N); palatine width (01-02); rostral width (B1-B2); third molar width (K1-K2); first premolar width (L1-L2); postpalatal length (P-S); auditory bulla length (Q1-Q2); auditory bulla width (R1-R2); greatest width of skull (G1-G2); mastoid breadth (H1-H2); least interorbital width (E1-E2); skull depth (F1-F2).

sions. Significant differences among locations for each character were analyzed by single classification analysis of variance tests and sums of squares simultaneous test procedure (SS-STP; Gabriel, 1964; Power, 1970). Multivariate analyses were performed using the subroutines from the NT-SYS (Rohlf *et al.*, 1974) and SAS (Barr *et al.*, 1976) computer programs. Matrices of Pearson's product-moment correlation coefficients between samples and characters were computed from standardized character values. Dendrograms of phenetic distance among samples and correlations among characters were prepared using the UPGMA (unweighted pair-group method using arithmetic averages) clustering method. The first three principal components and projections of samples were prepared from the matrix of phenetic distances and correlation among characters (Sneath and Sokal, 1973). Differences in cranial dimensions between the sexes were analyzed by single classification and multivariate analysis of variance. The proportion of character variability attributable to regional differences and intrapopulational variation was analyzed by variance components analysis (cf. Straney, 1976). Associations between matrices of phenetic distance and linear distance between localities were tested by Mantel's (1967; Sokal, 1979) general regression analysis (program from Chesser, 1980). The prairie dogs used in this study were also analyzed for electrophoretic variability in a previous study (Chesser, 1981). Classifications resulting from the phenetic and electrophoretic analyses were compared.

Results and Discussion

The cranial dimensions for male black-tailed prairie dogs were significantly larger than those for females for 15 of the 17 characters measured (Table 2). In addition, the multivariate analysis of variance using all skull characters indicated a highly significant difference between the sexes ($P < 0.001$). Pizzimenti (1975) reported that prairie dogs were slightly to moderately sexually dimorphic and chose to combine measurements for the two sexes in subsequent analyses (Pizzimenti, 1976). Tileston and Lechleitner (1966) reported that external measurements of male and female black-tailed prairie dogs did not differ. Because of the significant differences between sexes in this study, all subsequent analyses were performed for each sex separately. This procedure reduced the sample sizes for each population. However, the matrices of phenetic distances among samples calculated for each sex were significantly associated (Mantel test, $t = 2.02$, $P < 0.05$; matrix correlation $= 0.28$), and no great distortion of sample relationships was apparent due to the data reduction.

Significant heterogeneity among localities is evident for 12 of the 17 characters for males and 15 of 17 for females (see Appendix I of Chesser, 1981, for character means for each sample). Length of the maxillary toothrow, width of the third molar, auditory bulla width, and upper diastemal length showed the greatest amount of interlocality variation for males. For females, variation among localities was high for width of the third molar, greatest skull length, greatest width of the skull, and basilar length. No significant variation among populations was found for rostral length, premolar width, post-palatal length, length of the auditory bulla, and interorbital width for males; and none was found for palatine width and premolar width for females (results of SS-STP tests are given in Appendix II of Chesser, 1981).

Character variation among the 18 samples was summarized by extraction of principal components. Three-dimensional projections are presented in Figures 1B and 1C for males and females, respectively. The loadings (correlations) of each character with each of the first three principal components are given in Table 2.

TABLE 2.—*Mean value (in mm.) for each of 17 characters measured for male (M) and female (F) prairie dogs, and results of analysis of variance (F-ratio) tests for sexual dimorphism. The loadings of each character on the first three principal components for each sex are also given.*

				Principal components		
Character	Sex	Mean	*F*-ratio[1]	I	II	III
Skull length	M	6.25	65.63***	.961	−.111	.010
	F	6.07		.983	−.019	.085
Basal length	M	5.62	52.23***	.984	−.068	−.067
	F	5.44		.938	.235	.143
Rostral length	M	2.53	49.69***	.859	.053	.366
	F	2.26		.893	.130	−.053
Nasal length	M	2.37	49.98***	.717	.419	.375
	F	2.28		.838	−.404	.155
Diastemal length	M	1.54	12.65***	.702	.505	−.312
	F	1.51		.893	−.113	−.075
Toothrow length	M	1.62	7.23**	.117	−.834	.205
	F	1.60		−.185	.860	.168
Palatine width	M	0.88	1.85	.279	−.045	−.179
	F	0.87		.174	.164	−.836
Rostral width	M	1.13	1.36	.843	−.166	−.199
	F	1.12		−.035	−.035	−.902
Third molar width	M	0.39	5.02*	.621	.430	−.594
	F	0.38		−.063	−.204	.086
Premolar width	M	0.31	7.00**	.356	−.578	−.468
	F	0.30		.301	.229	−.344
Post-palatal length	M	2.23	29.64***	.834	.089	.194
	F	2.15		.890	−.345	−.011
Auditory bulla length	M	1.14	17.75***	.469	.449	−.187
	F	1.11		.488	.288	−.462
Auditory bulla width	M	1.04	12.66***	.823	−.132	.052
	F	1.01		.593	−.328	.172
Skull width	M	4.44	45.01***	.769	−.278	−.216
	F	4.29		.921	−.108	.102
Mastoid breadth	M	2.72	38.38***	.805	−.390	−.134
	F	2.64		.593	.682	.244
Interorbital width	M	1.33	20.37***	.490	.519	.494
	F	1.28		.401	.810	.072
Skull depth	M	1.92	71.66***	.634	−.380	.533
	F	1.86		.436	−.229	−.259

[1] Degrees of freedom for each test are 1,317.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

The values for the character loadings for males and females were generally similar. The amount of phenetic variation represented by the first three principal components for males and females, respectively, was: 49.6 and 42.6 for component I, 15.1 and 15.3 for component II, and 10.2 and 12.4 for component III. The total variability explained by the first three principal components was 74.9 for males and 70.3 for females.

Characters with high loadings on principal component I were ones that reflected the overall size of the skull. Measurements such as palatine width, premolar width, and auditory bulla width, as well as measurements of skull depth and least interorbital width, had low associations on the first component. Rostral width and third molar width had relatively high loadings for males but not for females. Samples which had large overall skull dimensions are depicted towards the right-hand side of Figs. 1B and 1C.

Component II had high loadings for maxillary toothrow length and greatest skull length for both males and females, mastoid breadth for females only, and premolar width and upper diastemal length for males. Maxillary toothrow length for females and premolar width for males had negative loadings. All of the other high loadings had positive values. Thus, females with relatively short toothrows, deep skulls, and wide mastoidal breadth are depicted towards the front of Fig. 1C; samples for males depicted near the front of Fig. 1B had narrow premolars, long toothrows, and large diastemal lengths.

Component III had high loadings for palatine width and rostral width and a moderately high value for length of the auditory bulla in females. Males had relatively high loadings for the third molar width, premolar width, skull depth, and least interorbital width. Samples for females from populations with low values for auditory bulla length, palatine width, and rostral width are depicted high above the base of Fig. 1C. In contrast, males with small premolar widths, deep skulls, and broad interorbital widths are illustrated by the points high on the figure.

Samples within the four regions did not fall into distinct clusters. The two populations within the Tularosa Basin, CARZ and ALAM, which together have been proposed as an endangered subspecies (Hansen, 1977), are widely separated (Figs. 1B, 1C). Prairie dogs from the ALAM population did have consistently larger cranial dimensions than animals from most other populations, but this large size was not shared by CARZ animals or those from the nearby Roswell region (ROS1 and ROS2; *C. l. arizonensis*). Neither morphological nor genic data (Chesser, 1981) for prairie dogs support the designation of all Tularosa Basin populations as a single endangered subspecies, and thus Hansen's (1977) classificatory recommendations are not supported by my findings.

In addition, *C. l. arizonensis* does not appear to possess any unique characteristics to substantiate a separate subspecies in this region of New Mexico. The strong variation among local populations poses some unique logistical problems for the systematic classification of organisms. The reason the Tularosa Basin prairie dogs and those of the Roswell region did not meet the criteria of a separate subspecies was not because they were found to be similar to other groups, but rather because all of the populations were apparently different and no distinct classification could be made. Thus, two options are available regarding the taxonomy of populations of prairie dogs: the first would be to designate a large number of subspecies of prairie dogs; the second and more tenable option is to lump them together as a single subspecies. Thus, the conclusions of this study are: (1) prairie dogs from the Tularosa Basin region do not constitute a separate subspecies, and (2) there is no basis for considering that the populations in the Roswell and Tularosa Basin regions represent a separate subspecies other than *C. l. l.* Conclusions regarding the status of the *C. l. a.* complex to the west and south of the Tularosa Basin cannot be made without further studies.

Differences of cranial morphology between populations separated by short distances were particularly evident for samples within Roosevelt County. Samples from populations separated by as little as 15 km. did not cluster together (e.g., CAUS-LING, HYWY-HYW2; Figs. 1B and 1C). Apparently, as was concluded in the genetic study (Chesser, 1981), differences between local populations are at times as great as those between populations in different regions. Factors such as the sedentary nature of prairie dogs (King, 1955), the disruption of continuous suitable habitat by ranching and agriculture (Koford, 1958), and the decimation of populations by poisoning practices (Collier and Spillett, 1975) may reduce successful dispersal among populations and enhance random differentiation. The low similarity in cranial morphology between neighboring populations was emphasized by the lack of association between matrices of phenetic and the reciprocal of linear geographic distances.

The results of the variance component analysis (Table 3) elucidate the relative importance of interlocality versus interregional sources of variability for cranial dimensions. The majority of the variability was not accounted for by samples compared within regions or samples compared between regions. Although the amount of variability accounted for by comparing samples within and between regions was at times considerably different for the two sexes, the overall means were similar. The amount of variation attributable to differences among locations was almost three times

TABLE 3.—*Percentage of morphological variability accounted for by differences among samples within regions (locations), among regions, and within locations for each of 17 skull characters measured for male and female black-tailed prairie dogs.*

Skull character	Males			Females		
	Within regions	Among regions	Within locations	Within regions	Among regions	Within locations
Skull length	15.4	3.1	81.5	23.0	4.3	73.7
Basal length	9.7	6.1	84.2	17.2	1.7	81.1
Rostral length	9.0	0.3	90.7	6.7	1.6	91.7
Nasal length	19.8	1.7	78.5	11.6	1.5	86.9
Diastemal length	1.8	15.9	82.3	13.3	2.2	84.5
Toothrow length	33.0	2.2	64.8	7.8	0.2	92.0
Palatine width	0.0	6.9	93.1	0.0	3.5	96.5
Rostral width	7.6	2.9	89.5	1.1	0.3	98.6
Third molar width	1.7	19.7	78.6	20.9	2.0	77.1
Premolar width	14.5	0.2	85.3	2.6	0.3	97.1
Post-palatal length	8.7	1.6	89.7	9.4	4.2	86.4
Auditory bulla length	0.0	3.7	96.3	0.0	9.0	91.0
Auditory bulla width	25.0	0.2	74.8	17.8	3.5	78.7
Skull width	12.6	1.3	86.1	15.0	7.7	77.3
Mastoid breadth	8.3	2.5	89.2	9.6	2.2	88.2
Interorbital width	2.1	0.4	97.5	8.3	3.3	88.4
Skull depth	8.2	4.2	87.6	10.4	2.2	87.4
Mean	10.4	4.3	85.3	10.3	2.9	86.8

greater than that among the four regions for all cranial characters except upper diastemal length and width of the third molar for males, and palatine width and auditory bulla length for both males and females.

The average amount of morphometric variability explained by location within regions and among regions was almost identical to the amount of gene diversity (Nei, 1975) explained by these same two sources of variation (Chesser, 1981, location = 10.31%; region = 3.56%). Even though the patterns of variability for morphometric and electrophoretic data were similar, the matrices of phenetic and genetic distances between populations were not significantly associated (*P* >0.30 for both males and females; *P* > 0.20 when data for males and females were combined). Thus, as in the case for kangaroo rats (Schnell *et al.*, 1978), classifications based on skeletal and electrophoretic data are not consistent. If stochastic factors were the primary causes for producing the differences among populations with little or no dispersal between them, the distributions of phenetic and genetic variabilities may be expected to be similar. Stochastic and/or selective forces probably affect phenetic and electrophoretic characters differently (e.g., Wright, 1980). Thus, systematic relationships between populations based on the two types of data may not be associated, whereas the overall amounts of variation among samples may be comparable.

The conclusions of this study are similar to those from the author's (Chesser, 1981) genetic analysis of prairie dogs. There is considerable variation among samples in close proximity, and the intraregional variability is far more pronounced than that found between regions. No geographic or subspecific relationships are evident. Erratic geographic variation among samples is not unusual, especially when populations are somewhat isolated and the possibility of reciprocal genetic exchange is or has been limited (Berry *et al.*, 1978; Choate and Williams, 1978). The distribution of prairie dogs was somewhat continuous 75 to 100 years ago before poisoning and agricultural practices reduced their range (Seton, 1929). It is doubtful, however, that all phenetic and genetic differentiation has taken place since that time. Prairie dogs have probably always had disjunct patterns of variation due to their complex social organization and low dispersal rates (King, 1955), and the high degree of variation among nearby samples hinders the identification of variables that would characterize distinct subspecific groups.

The above arguments do not rule out the possibility of significant geographic trends. If samples were analyzed over the entire range of black-tailed prairie dogs, significant regional trends would probably be evident (cf. Pizzimenti, 1975); however, the variation within any specific region would most likely be similar to that described in this paper. The classical definition of a subspecies (e.g., "an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the speecies and differing taxonomically from other populations of the species"; Mayr, 1963, p. 210) is probably not applicable to prairie dogs. Progressive reduction of the distribution of prairie dogs to scattered, isolated populations within all portions of its range will continue to enhance local differentiation of populations.

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OCCURRENCE OF BAIOMYS TAYLORI (RODENTIA: CRICETIDAE) ON THE TEXAS HIGH PLAINS

FREDERICK B. STANGL, JR., BEN F. KOOP, AND CRAIG S. HOOD

To our knowledge, no published records exist that document the presence of the pygmy mouse, *Baiomys taylori*, on the High Plains of Texas. However, a specimen trapped on 23 January 1982 revealed the occurrence of this species at a place 4 mi. E Southland, in Garza County. The area is along the upper rim of the escarpment of the Llano Estacado where the surrounding terrain is rough and rocky. Here the mouse was taken in a mesquite-grassland habitat in association with *Sigmodon hispidus*, *Reithrodontomys montanus*, *Onychomys leucogaster*, *Peromyscus leucopus*, *P. maniculatus*, and *Neotoma micropus*. A subsequent search of the mammal collection of The Museum, Texas Tech University, produced other noteworthy records, which also are reported here.

A single specimen was obtained 10 mi. S Post, also in Garza County, on 2 February 1980. The animal was captured by hand in one of many prickly-pear nests of *Neotoma* that were dismantled during a collecting trip by mammalogy students from Texas Tech University. Also collected by this method on that day were *Notiosorex crawfordi*, *Neotoma micropus*, *Peromyscus leucopus*, and *Sigmodon hispidus*. That locality, at the foot of the escarpment, is mesquite-grassland, associated with dense stands of prickly-pear cactus (*Opuntia* sp.). Surrounding terrain has considerable relief and soils are hardpan and rocky.

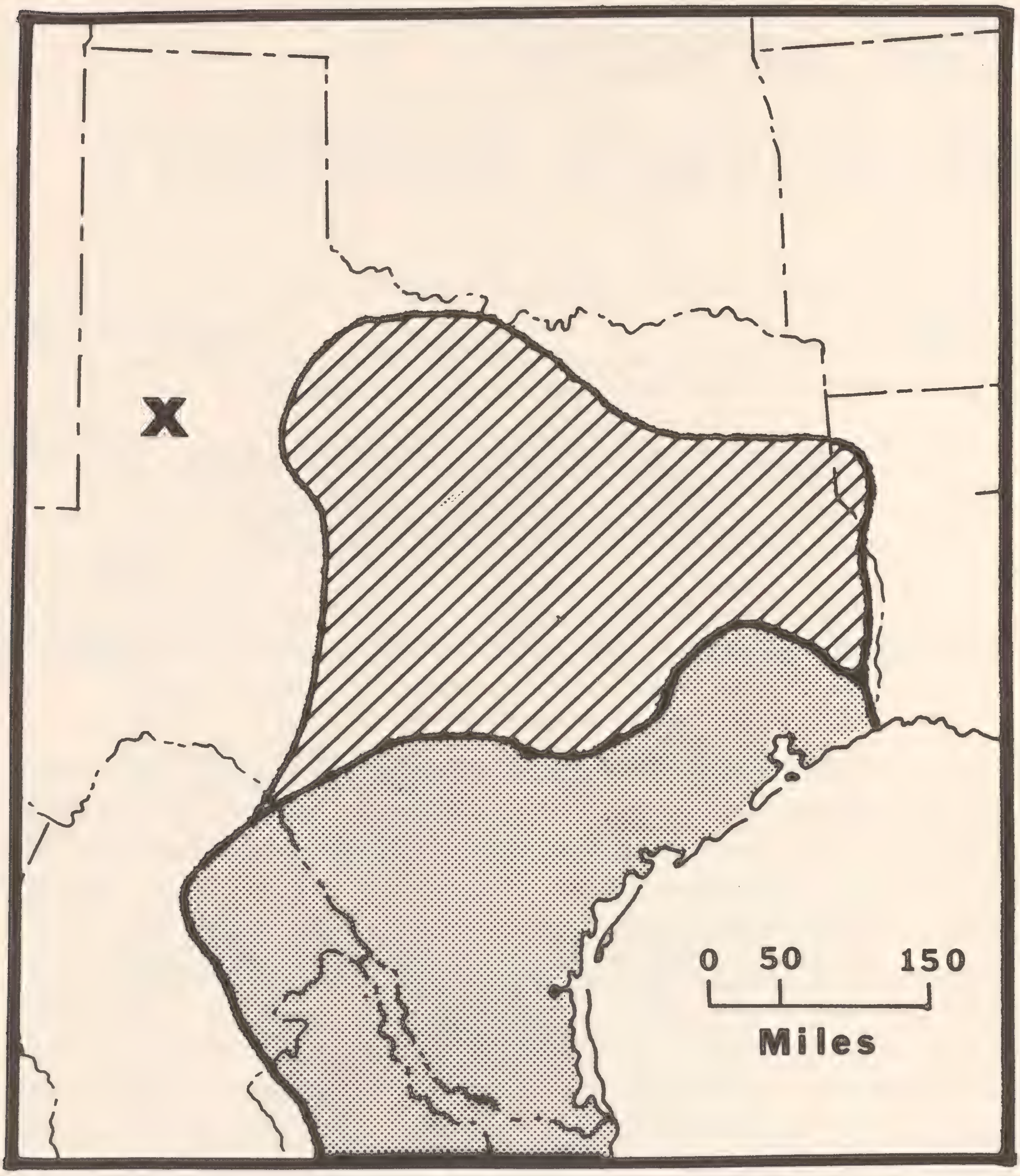

FIG. 1.—Known range extension of *Baiomys taylori* since 1959. Stippled area indicates range of the pygmy mouse in Texas according to Hall and Kelson (1959). Diagonal lines show range extension of the species, from Hall (1981). "X" indicates the approximate location of new records for *Baiomys* in the state.

A series of six pygmy mice was collected 4 mi. N and 1 mi. E Slaton, in Lubbock County, one specimen taken on 27 February 1977 and five on 7 March 1977. That locale is situated in rough, rocky terrain where mesquite-grassland association occurs.

On 7 March 1977, a *Baiomys* was taken at Buffalo Springs Lake, 4 mi. S, 7 mi. E Lubbock, Lubbock County. This is the northwesternmost record of *Baiomys taylori*.

Pygmy mice are typical inhabitants of low grassy or weedy areas (Davis, 1974). The range of the species in Texas, as currently

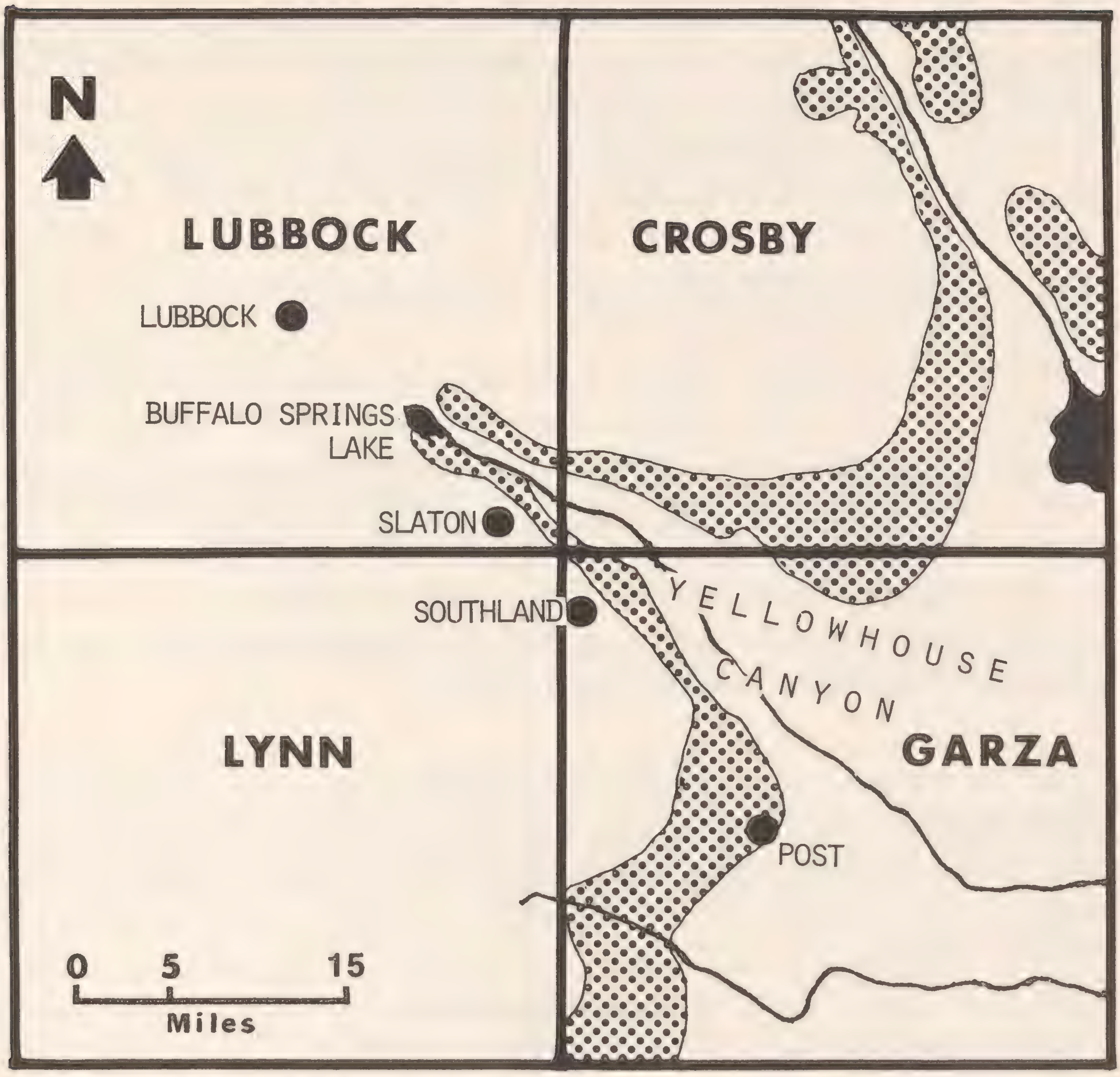

FIG. 2.—Four-county map of reference points for new records of *Baiomys taylori*. Escarpment (stippled area) separates the Texas High Plains of the west from the lower Gypsum Plains to the east.

understood, occupies southern, central, and north-central parts of the state (Hall, 1981; and Davis, 1974). Packard and Garner (1964), in a listing of mammalian range extensions for the Texas High Plains, mentioned only the addition of a specimen from Mason County. Packard and Judd (1968) later provided other northwesterly range extensions of *B. taylori* within the state, and suggested that the species was gradually extending its distribution.

The extent of recent expansion of known range of this species to the north and northwest is shown in Fig. 1. New records reported herein reveal that *Baiomys taylori* now has reached the edge of the High Plains by way of shallow canyons leading down from that region to the Gypsum Plains to the east. Packard and Judd (1968) and Packard and Garner (1964) suggested that these canyons serve as avenues of dispersal for other mammals as well.

Yellowhouse Canyon, forged by the Double Mountain Fork of the Brazos River, appears just such a dispersal route (see Fig. 2). The mouth of this canyon is situated near the previously mentioned collecting sites near Post, in Garza County. The head of the canyon is located near Buffalo Springs Lake in Lubbock County, another locale from which *B. taylori* is known. Places near Southland and Slaton where the pygmy mouse has been collected also are along Yellowhouse Canyon.

Further expansion westward across the High Plains appears unlikely where such canyons meet areas of intense agricultural activities, as occur in Lubbock and Garza counties. However, further trapping and investigation along the escarpment and accompanying canyons may yet reveal more distribution records for the pygmy mouse. Where such canyons originate in areas of suitable habitat, the species might be expected to continue its westward expansion into the High Plains.

ACKNOWLEGMENTS

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HISTOMORPHOLOGY OF THE FEMALE REPRODUCTIVE TRACT IN PHYLLOSTOMOID BATS

Craig S. Hood and James Dale Smith

Studies on the female reproductive organs of Chiroptera have shown that bats possess an amazing diversity of anatomical and functional specializations compared to other groups of mammals (Rasweiler, 1979*a*; Wimsatt, 1975, 1979). Bats possess more variation in uterine morphology than any other mammalian order; pteropodids and emballonurids have primitive duplex uteri, whereas bicornuate and simplex uterine morphologies have evolved within other chiropteran families (Mossman, 1977). Despite this diversity in uterine morphology, there has been little synthesis towards a general understanding of the evolution of this complex organ in bats.

Robin (1881) was apparently the first to provide a comparative morphological study of female genitalia in bats. He examined 45 species of 10 currently recognized families and documented the tremendous diversity in the gross morphology of the chiropteran uterus. Although he did not comment extensively on the phylogenetic implications of his findings, Robin suggested that some phylogenetic relationships could be predicted on the basis of uterine morphology. Wood Jones (1917) considered female internal and external genitalia in 19 species of eight currently recognized families. He proposed that several types of uteri are found among families of bats. The duplex uteri of pteropodids and the highly fused uteri of phyllostomids (including mormoopids) were established as unique extremes among these types. Although the duplex uterus of pteropodids is distinct compared to that found in most other bat families, it is apparently a primitive uterine morphology and, as such, does little to resolve phylogenetic relationships among bats. On the other hand, the uteri of the New World families Noctilionidae, Mormoopidae, and Phyllostomidae appear to be uniquely derived among bats. If the highly fused uterus of these chiropteran families represents a shared-derived feature, then it predicts a close phylogenetic relationship for noctilionids, mormoopids, and phyllostomids.

The systematic relationships of noctilionids, mormoopids, and phyllostomids have been studied extensively in recent years. Several independent data sets suggest that these bats share uniquely derived features that indicate close phylogenetic relationships (Walton and Walton, 1968; Smith, 1972, 1976; Patton and Baker, 1978; Luckett, 1980). On the basis of these shared-derived features, recent authors have regarded noctilionids, mormoopids, and phyllostomids as members of a monophyletic group, and have placed them in the superfamily Phyllostomoidea (for use of superfamilial and familial names, see Handley, 1980).

The present paper reports the results of a comparative histomorphological study of the uterus, oviducts, and ovaries in the New World families Noctilionidae, Mormoopidae, and Phyllostomidae. The reproductive biology of noctilionids and phyllostomids has been well studied in only six genera, including *Noctilio* (Anderson and Wimsatt, 1963; Rasweiler, 1977, 1978), *Desmodus* (Wimsatt, 1954; Wimsatt and Trapido, 1952; Quintero and Rasweiler, 1974), *Macrotus* (Bradshaw, 1962; Bodley, 1974; Bleier, 1975) *Glossophaga* (Hamlett, 1935; Rasweiler, 1972, 1974, 1979*b*), *Carollia* (Bonilla and Rasweiler, 1974), and *Artibeus* (Wislocki and Fawcett, 1941; Tamsitt and Valdivieso, 1963, 1965; Fleming, 1971). Virtually no information exists on the reproductive biology of mormoopids (Wimsatt, 1979).

The purpose of this paper is to present a comparative data set on reproductive histomorphology of phyllostomoid bats. It is hoped that this study will provide a stimulus for future research on the reproductive biology of individual species. In addition, because phylogenetic relationships of these three families have been well studied through several independent data sets, the usefulness of female reproductive histomorphology in testing phylogenetic hypotheses can be assessed. Phylogenetic implications are treated in detail elsewhere (Hood and Smith, 1982).

MATERIALS AND METHODS

Specimens used in this study were obtained from natural populations. Whole female reproductive tracts were excised, then fixed in Zenker's or Bouin's solution

(Humason, 1972). Reproductive tracts also were removed from formalin-fixed museum specimens. The quality of fixation in this latter material varied greatly; in many cases only general anatomical relationships could be ascertained. The reproductive status of individuals used in this study included most stages of the female cycle. Many specimens had early-implanted blastocysts, although some late-pregnant uteri also were examined. The former condition is especially informative regarding oviductal histomorphology and in defining sites of implantation (Rasweiler, 1977, 1979*a*). Specimens in later stages of pregnancy were less useful in describing uterine morphology because of displacement or destruction of tissues by the developing embryo.

Histological Procedures

Tissues were processed through paraffin, serially sectioned at 6-8 micra, and stained with Mallory's Trichrome (Humason, 1972) or Gomori's One Step Trichrome Method (Thompson, 1966:788). The Gomori Trichrome staining method is capable of discriminating epithelial, connective, muscular, and vascular tissues and has been applied to the study of complex organs (Bhatnagar and Kallen, 1974; Bhatnagar, 1980; Smith and Madkour, 1980). Organization of connective tissues is especially well demonstrated by the light green component of the stain, a feature important for detailing oviductal penetration into the uterus (see Rasweiler, 1974, for a similar discussion concerning Masson's Trichrome). One modification of the Gomori Method was found to improve our results. The standard treatment with hot Bouin's solution (56°C) for one hour frequently led to sections loosening from the slides. This undesirable effect was remedied by substituting this treatment with 12 to 18 hours in room temperature (20°C) Bouin's solution; staining intensity was maintained with excellent clarity.

Most of the reproductive tracts were sectioned in the frontal plane although a few were prepared in transverse section. Reconstruction of the histomorphology of the female reproductive organs was accomplished by examination of serial sections. Each reproductive tract, so examined, was compared to photographs and/or drawings taken before the specimen was prepared histologically.

Out-group Comparison and Phylogenetic Characters

One of the goals of comparative studies is to present primary descriptive accounts that can be used to assess phylogenetic relationships. A logical framework for the testing of phylogenetic hypotheses has been presented by Hennig (1966) and discussed by Smith (1980). Luckett (1980) has emphasized three important aspects of phylogenetic character analysis. These include: 1) determining the homologous or homoplastic nature of shared similarities among organisms; 2) identifying and arranging character states into transformation series; and 3) determining the relative primitive or derived nature of these character states.

In the present paper, histomorphological features are described and are hypothesized as primitive (plesiomorphic) or derived (apomorphic) on the basis of the out-group comparison method (Watrous and Wheeler, 1981). This will provide a basis for subsequent cladistic analyses. Representatives from the following chiropteran families were examined as out-groups to noctilionids, mormoopids, and phyllostomids: Pteropodidae, Emballonuridae, Rhinolophidae, Hipposideridae, Vespertilionidae, Mystacinidae, and Molossidae. Literature reports were used to determine character distributions in other eutherian orders.

Specimens Examined

Reproductive tracts (116) of the following taxa were examined (numbers in parentheses indicate sample size): PTEROPODIDAE: *Rousettus amplexicaudatus* (2); *Nyctimene albiventer* (2); *Eonycteris spelaea* (2); *Macroglossus lagochilus* (2); *M. minimus* (2); EMBALLONURIDAE: *Rhynchonycteris naso* (1); *Balantiopteryx plicata* (2); *Taphozous longimanus* (1); *Saccopteryx bilineata* (3); RHINOLOPHIDAE: *Rhinolophus denti* (1); HIPPOSIDERIDAE: *Hipposideros caffer* (1); *H. diadema* (2); NOCTILIONIDAE: *Noctilio albiventris* (3); *N. leporinus* (1); MORMOOPIDAE: *Pteronotus macleayi* (2); *P. parnellii* (6); *P. quadridens* (3); *Mormoops blainvillii* (1); PHYLLOSTOMIDAE: (Phyllostominae) *Micronycteris hirsutus* (1); *M. megalotis* (1); *Macrotus californicus* (4); *Phyllostomus discolor* (4); *P. hastatus* (1); *Phylloderma stenops* (1); *Trachops cirrhosus* (1); (Glossophaginae) *Glossophaga soricina* (3); *Monophyllus redmani* (1); *Leptonycteris curasoae* (2); *Lonchophylla robusta* (2); *Anoura geoffroyi* (1); (Carolliinae) *Carollia castanea* (1); *C. perspicillata* (3); *C. subrufa* (1); *Rhinophylla pumilio* (3); (Stenoderminae) *Sturnira lilium* (4); *Uroderma bilobatum* (2); *Vampyrops helleri* (2); *Vampyrodes caraccioli* (1); *Vampyressa pusilla* (3); *Ectophylla alba* (1); *Artibeus jamaicensis* (4); *Enchisthenes hartii* (1); *Ariteus flavescens* (1); *Ametrida centurio* (1); *Centurio senex* (2); (Brachyphyllinae) *Brachyphylla cavernarum* (1); *Phyllonycteris aphylla* (3); (Desmodontinae) *Desmodus rotundus* (2); VESPERTILIONIDAE: *Myotis adversus* (1); *M. californicus* (2); *M. evotis* (2); *M. emarginatus* (1); *M. lucifugus* (1); *Pizonyx vivesi* (1); *Pipistrellus hesperus* (3); *Rhogeessa tumida* (1); *Scotophilus kuhlii* (1); *Plecotus townsendii* (1); *Antrozous pallidus* (1); MYSTACINIDAE: *Mystacina tuberculata* (2); MOLOSSIDAE: *Tadarida braziliensis* (1); *T. plicata* (1); *Eumops trumbulli* (1); *Molossus molossus* (1).

UTERINE HISTOMORPHOLOGY

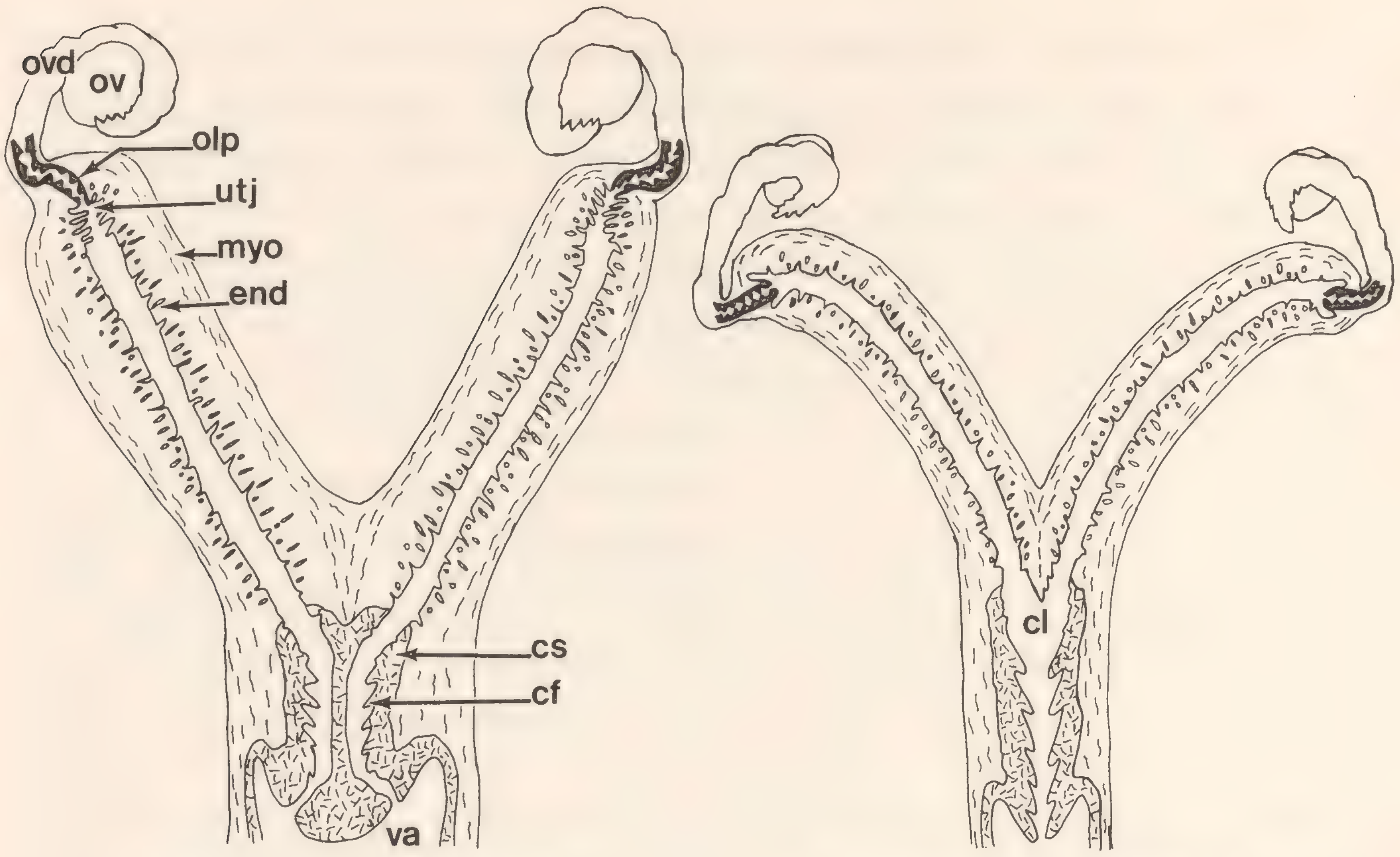
General Description

The mammalian uterus is a complex, tubular organ which varies considerably in gross morphology. The primitive eutherian uterus is hypothesized to have consisted of two uterine horns (cornua); these open independently into the vagina (Mossman, 1977). Some members of the Chiroptera (see below), Dermoptera, Lagomorpha, and Rodentia have retained this primitive arrangement, whereas derived uterine morphologies have evolved independently in many mammalian orders. Derived morphologies apparently have developed by progressive, caudal to cranial fusion of the uterine horns resulting in the formation of a median, common uterine body. This progression involves two aspects of the uterine horns: 1) superficial tissues of the cornua fuse, and 2) following this external fusion, the internal uterine lumina may become confluent by degeneration of the median septum. However, it is possible that the internal uterine anatomy may be retained in a relatively primitive separated condition despite external fusion of the uterine cornua.

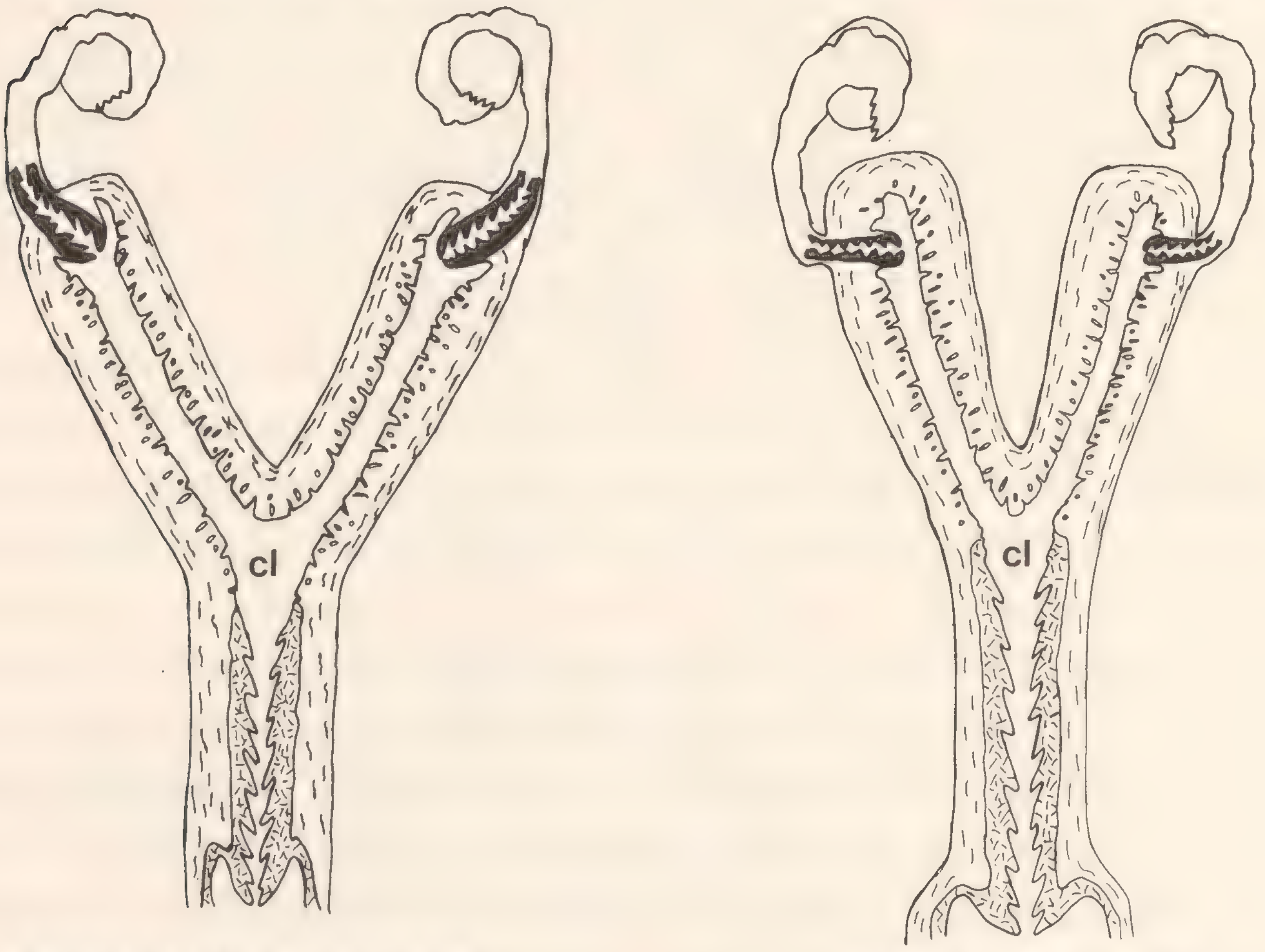
On the basis of gross morphology, both primitive and derived uteri are found within the Chiroptera. All chiropteran families examined in this study (except phyllostomoids) have relatively long uterine horns and moderately short, common uterine bodies. In contrast, the uteri of noctilionids, mormoopids, and phyllostomids have short uterine horns and a prominent, common uterine body; most phyllostomids have a completely simplex uterus.

The mammalian uterus is composed of three histologically well-defined tissue layers. An outer serosa is continuous with the peritoneum and, together with associated mesenteries and ligaments (broad, round, and suspensory), supports the uterus. The thick, middle tunic (myometrium) is comprised of smooth muscle fibers; this layer constitutes a large portion of the uterine wall. The innermost layer (endometrium) is a mucosa of simple columnar epithelium with associated glands, supported by an underlying connective tissue (lamina propria). The endometrium undergoes marked cyclic changes during reproduction. The caudal end of the uterus constitutes the cervix; this region has a distinct mucus-secreting epithelium and a dense connective tissue stroma. Cervical histomorphology has been discussed at length in a number of mammalian orders, including primates, rodents, carnivores, and artiodactyls (Hafez and Jaszczak, 1972; Hafez, 1973*a*; Graham, 1973; Kanagawa and Hafez, 1973). Caudally, the cervix projects into the vagina as a rounded or conical mound—the portio vaginalis. The cervicovaginal junction is abrupt in most mammals, but varies considerably within primates and bats (Graham, 1973; this study).

In all chiropteran families examined in this study, the free uterine horns were comprised of well-defined myometrium and endometrium; these uterine tissues constitute the gestational portion of the uterus. On the other hand, the common uterine body is comprised of two histologically distinct regions. These include an endometrial-lined gestational portion and the cervix. In the pteropodids and emballonurids examined in this study, the common uterine body is extremely short. The cervix constitutes most of this externally fused portion, whereas only a small amount of the gestational uterus is involved. In all other chiropteran families examined (except phyllostomoids), the common uterine body is longer, but, nonetheless, it is mostly comprised of cervical tissue (Fig. 1). However, in noctilionids, mormoopids, and phyllostomids, the common uterine body is extremely large; the gestational uterus constitutes a major portion, whereas the cervix is limited to

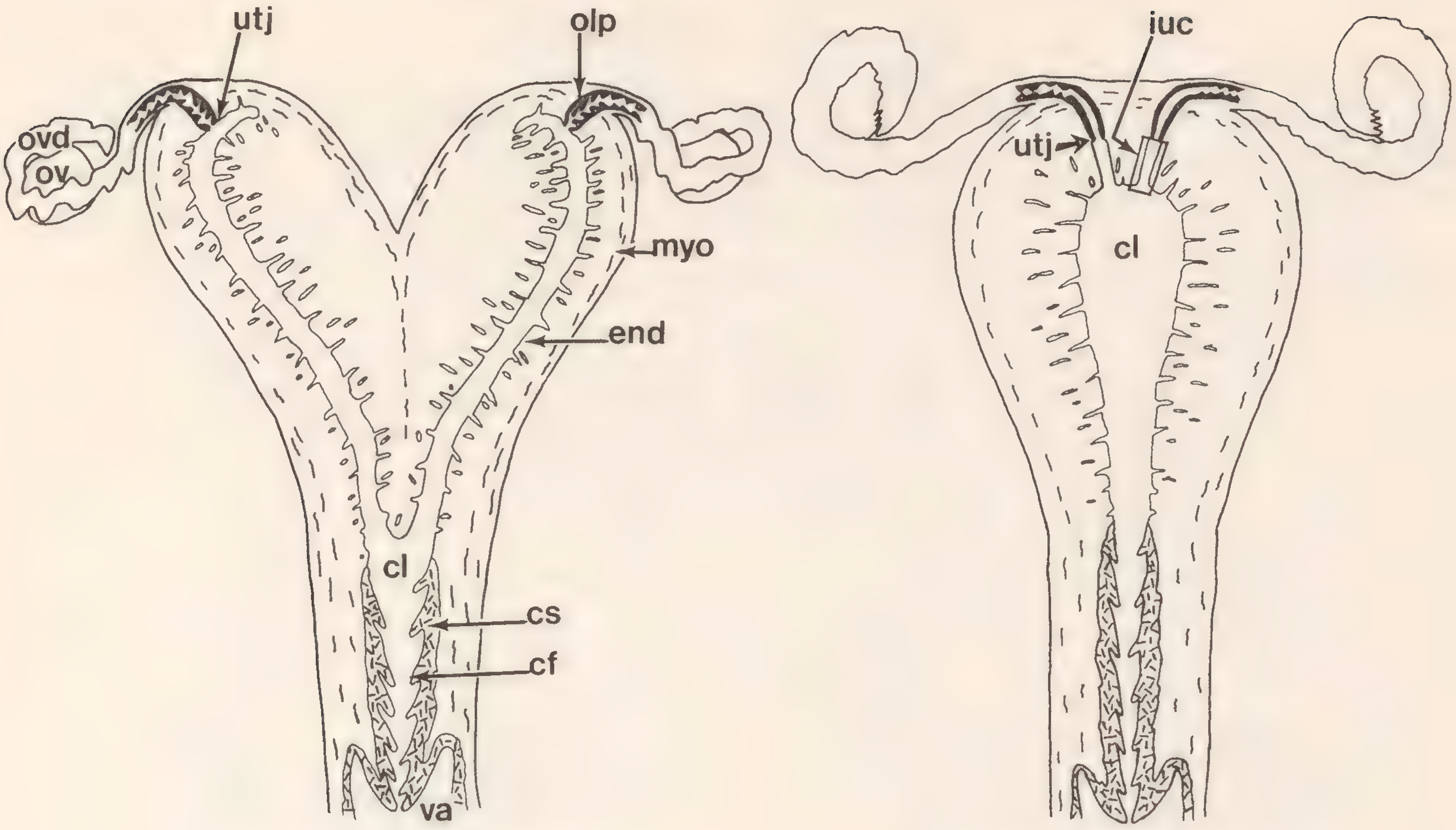


TAPHOZOUS LONGIMANUS HIPPOSIDEROS DIADEMA



PIPISTRELLUS HESPERUS TADARIDA PLICATA

FIG. 1.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries of representative chiropteran families, including Emballonuridae: *Taphozous longimanus*; Hipposideridae: *Hipposideros diadema*; Vespertilionidae: *Pipistrellus hesperus*; Molossidae: *Tadarida plicata*. The oviductal lamina propria is shaded to outline the oviduct as it contacts and enters the uterus and to indicate the depth of penetration of the intramural junctura. *Abbreviations:* **ov**, ovary; **ovd**, oviduct; **olp**, oviductal lamina propria; **utj**, uterotubal junction; **myo**, myometrium; **end**, endometrium; **cs**, cervical stroma; **cf**, cervical folds; **va**, vagina; **cl**, common uterine lumen.



NOCTILIO ALBIVENTRIS

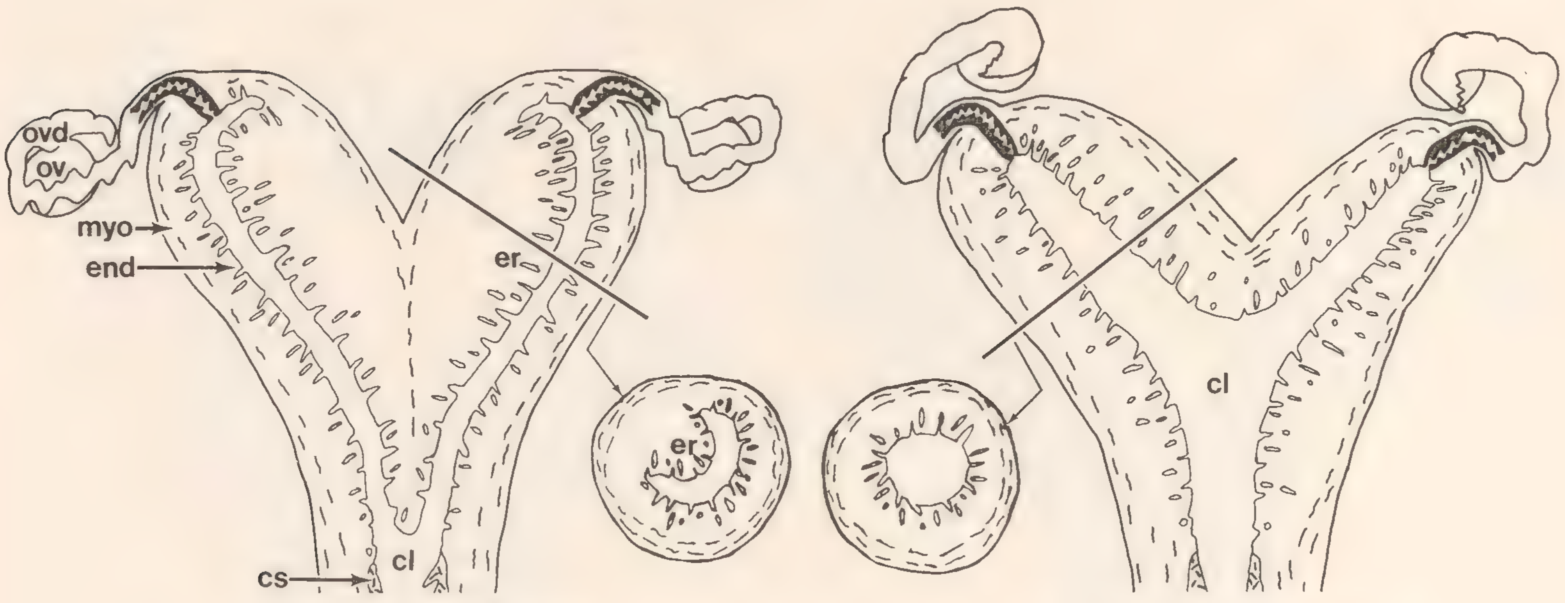
GLOSSOPHAGA SORICINA

FIG. 2.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries of phyllostomoid bats. *Noctilio albiventris* represents phyllostomoids that have a bicornuate uterus, whereas *Glossophaga soricina* is representative of phyllostomoids with a simplex uterus. The presence of tubular, intramural uterine cornua (**iuc**) is a unique feature of the phyllostomoid simplex uterus. Abbreviations can be found in Fig. 1.

the caudal end of the uterus (Fig. 2). This external uterine anatomy, and predominately gestational common uterine body, is considered a shared-derived (synapomorphic) feature of phyllostomoid bats.

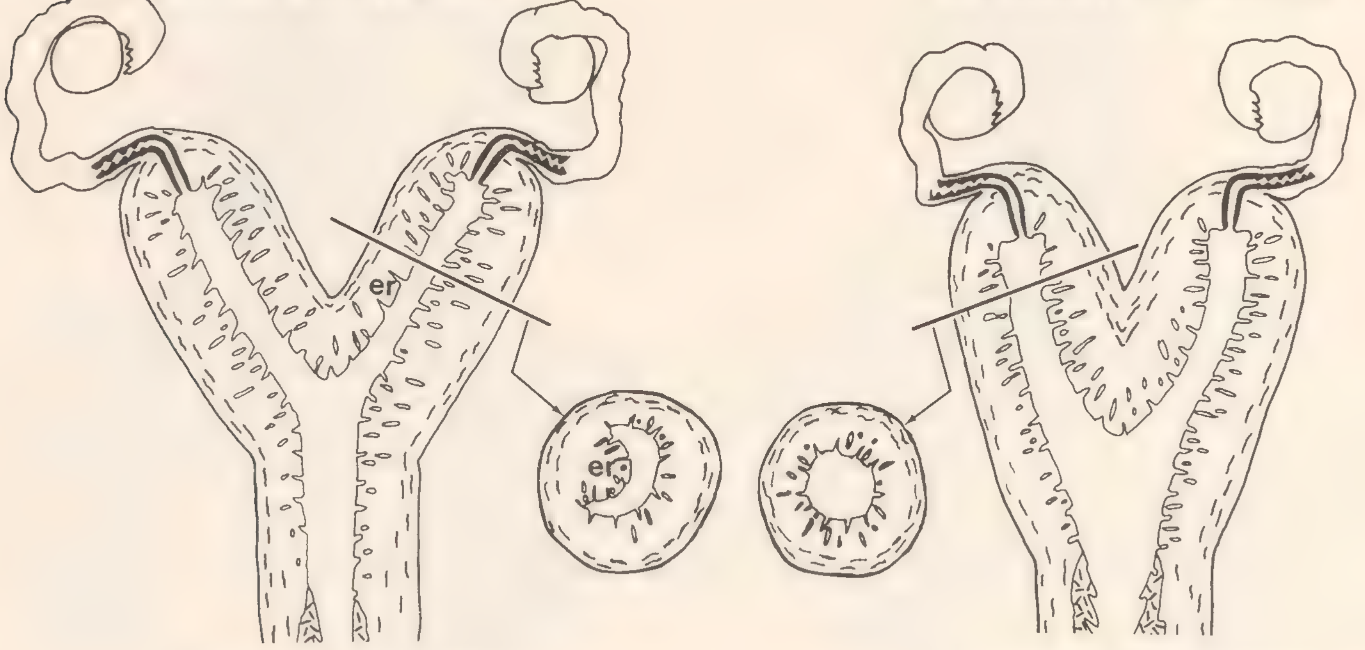
Cervical histomorphology of phyllostomoid bats is typical by eutherian standards; the cervical canal has a distinct mucous-secreting epithelium which is thrown into prominent cervical folds. All phylostomoid bats have a rounded or conical portio vaginalis and a clearly defined cervicovaginal junction.

Internally, all pteropodids examined to date and *Taphozous longimanus* (family Emballonuridae) have completely separate uterine lumina; these have two cervical openings into the vagina (Fig. 1). In all other chiropteran taxa examined, the uterine lumina join within the common uterine body forming a single canal and cervical opening. In the emballonurids *Rhynchonycteris, Balantiopteryx*, and *Saccopteryx*, rhinolophids, hipposiderids, and *Mystacina* (family Mystacinidae), this common uterine lumen is limited to the cervix, whereas in vespertilionids and molossids there is a short portion which is lined with gestational uterine tissue (Fig. 1).



NOCTILIO ALBIVENTRIS

PTERONOTUS PARNELLII



DESMODUS ROTUNDUS

MACROTUS CALIFORNICUS

Fig. 3.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries in representative bicornuate phyllostomoids, including Noctilionidae: *Noctilio albiventris*; Mormoopidae: *Pteronotus parnellii*; Desmodontinae: *Desmodus rotundus*; Phyllostominae: *Macrotus californicus*. A unique feature of *Noctilio* and *Desmodus* is the presence of an endometrial ridge (**er**) in the antimesometrial walls of the uterine cornua. Abbreviations can be found in Fig. 1.

Among phyllostomoid bats, noctilionids have retained markedly separate uterine lumina (Fig. 2). This internal uterine anatomy is similar to that of several chiropteran out-groups (see especially vespertilionids and molossids) and is considered a retained primitive (plesiomorphic) feature for phyllostomoids. On the other hand, the internal uterine anatomy in mormoopids and phyllostomids consists of a large endometrial-lined common uterine lumen; this fused internal anatomy is herein considered a synapomorphy of these two families (Fig. 3). In the systematic accounts that follow, variations in external and internal uterine anatomy among phyllostomoid bats are considered.

Family Noctilionidae

This Neotropical bat family includes those bats that are referred to as the bull-dog bats or fishing bats. It includes two species in one genus, *Noctilio* (Corbet and Hill, 1980).

The uterus of *Noctilio albiventris* has been described in detail by Anderson and Wimsatt (1963) and we confirm their results. The uterine cornua are short and bulbous, with a prominent common uterine body. Internally, the uterine lumina are not fused throughout the entire length of the common body. An extremely short common lumen is formed just cranial to the cervix. Anderson and Wimsatt (1963) noted that a ridge exists in the antimesometrial walls of the cornua; these ridges serve as sites of implantation (Fig. 3; Rasweiler, 1978, 1979*a*). It will be noted below that endometrial ridges are also found in the vampire bat, *Desmodus rotundus*.

The one specimen of *Noctilio leporinus* examined in this study had histomorphological features identical to that described above for *N. albiventris*. This specimen possessed an early-implanted blastocyst near the cranial end of an endometrial ridge. This site of implantation is similar to that observed in *N. albiventris*.

In noctilionids, the degree of fusion of the external uterine horns is shared with mormoopids and *Desmodus*. Other phyllostomids have uterine morphologies that are further specialized. On the other hand, the relatively separate internal uterine anatomy of *Noctilio* is shared with other chiropteran families examined herein.

Family Mormoopidae

The bats of this family are called moustached, naked-backed, or ghost-faced bats. These include two genera (*Pteronotus* and *Mormoops*) and eight species; all live in the Neotropics (Smith, 1972).

The uterine histomorphology of this family has not been described previously. Externally, both *Pteronotus* and *Mormoops* have relatively short uterine horns and a prominent common uterine body (Fig. 3). The cornua are markedly asymmetrical, the right side being anatomically and physiologically hypertrophied (Wimsatt, 1979:346, table 1; this study). The enlarged right uterine horn is similar in size and shape to both symmetrical horns of *Noctilio* (Fig. 3).

Unlike noctilionids, the internal uterine lumina are fused throughout most of the length of the common uterine body forming a large common lumen. In one specimen of *Pteronotus par-*

nellii, an early-implanted blastocyst was found in the cranial end of the right cornua. The blastocyst was implanted in the antimesometrial wall; however, orientation of the embryonic mass was not determined. Endometrial ridges were not noted in either horn of any mormoopid examined (Fig. 3).

Family Phyllostomidae

Bats of this family are referred to as New World leaf-nosed bats. This is an especially diverse family, including six subfamilies, 49 genera, and 143 species. All live in the New World tropics and subtropics (Jones and Carter, 1976).

Uterine morphology in phyllostomids is extremely diverse and illustrates progressive fusion of both external and internal uterine anatomy. Patterns of variation in phyllostomid subfamilies are considered in detail below.

Subfamily Desmodontinae.—This subfamily includes the true vampires; three monotypic genera include *Desmodus*, *Diaemus*, and *Diphylla*. Anatomical and behavioral adaptations for sanguivory (blood feeding) have led many researchers to regard the vampires as a separate and distinct family, albeit related to phyllostomids. However, this and other recent studies suggest that these bats are within the context of the Phyllostomidae (Machado-Allison, 1967; Forman *et al.*, 1968; Smith, 1972).

The reproductive biology of *Desmodus rotundus* has been studied extensively (Wimsatt, 1954; Wimsatt and Trapido, 1952; Quintero and Rasweiler, 1974). Compared to other phyllostomids, the uterine histomorphology of desmodontines is primitive. Externally, the uterus of *Desmodus* has short uterine horns and a long, common uterine body (Fig. 3). The cornua are symmetrical and tubular, and join to form a common uterine body which is only as wide as either horn. Overall, this uterus is distinctly Y-shaped.

The internal uterine lumina join immediately within the common uterine body forming a large common lumen. This internal anatomy agrees with that described above for mormoopids. A low endometrial ridge exists in the antimesometrial walls of the cornua (Fig. 3); as in *Noctilio*, these ridges serve as a site of implantation (Quintero and Rasweiler, 1974).

Subfamily Phyllostominae.—This subfamily includes bats that are known as big-eared, round-eared, sword-nosed, and spear-nosed bats. It includes 11 genera and 34 species that are widely distributed in the New World tropics and subtropics.

Based on uterine histomorphology, members of this subfamily can be arranged in two distinct groups. *Macrotus californicus, Micronycteris hirsutus, M. megalotis,* and *Trachops cirrhosus* possess uteri with extremely short cornua and a prominent, common uterine body; these taxa are herein referred to as the *Macrotus*-group (Fig. 3). Compared to other bicornuate phyllostomoids (i.e., noctilionids, mormoopids, and *Desmodus*), the external cornua are additionally fused. This external uterine anatomy is considered a synapomorphy of the *Macrotus*-group and other phyllostomids exclusive of *Desmodus*. Internally, the uterine lumina join to form a large common uterine lumen; internal uterine anatomy is similar to that observed in mormoopids and *Desmodus* (Fig. 3).

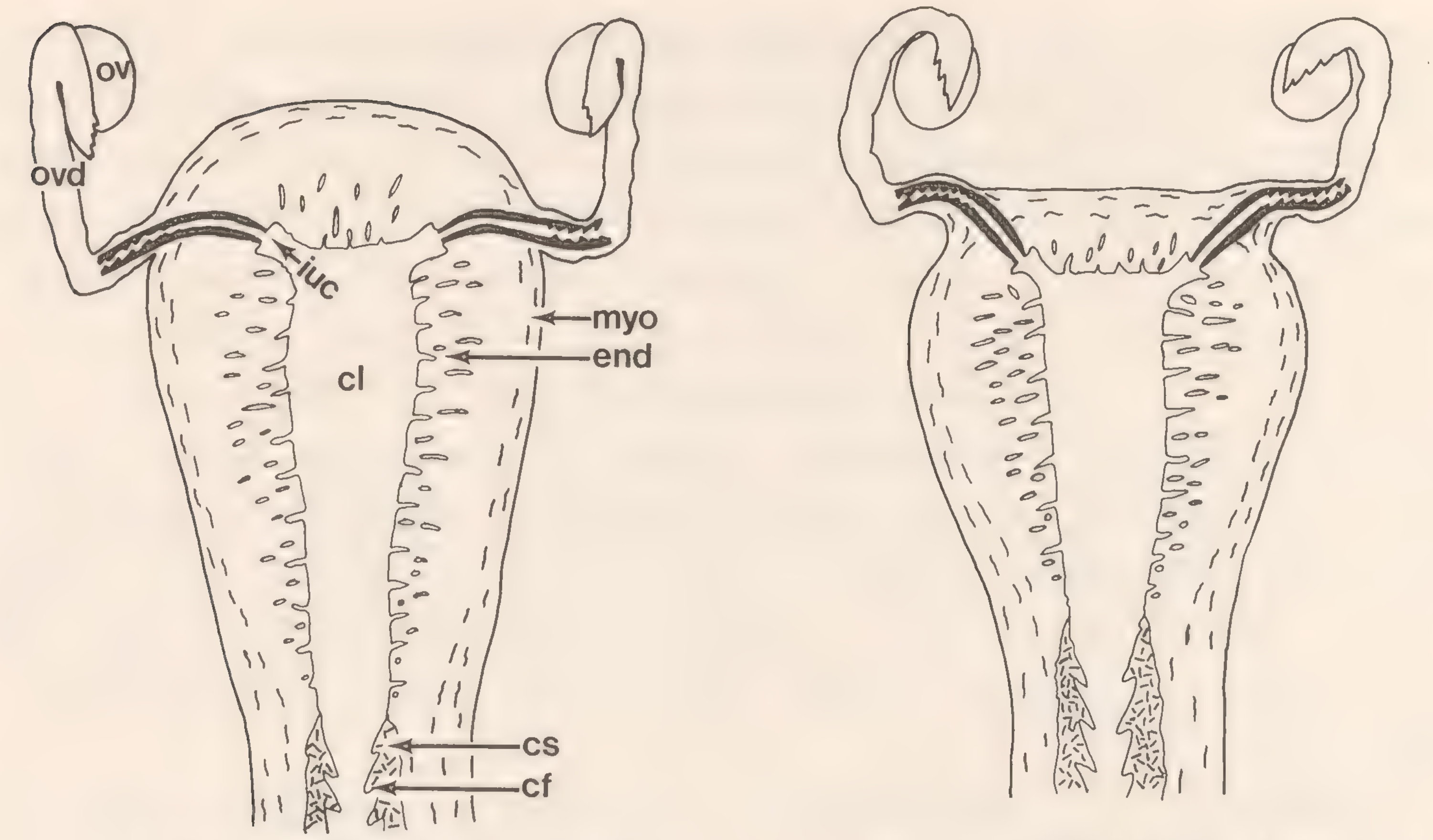
Anatomical and physiological asymmetry has been noted in *Macrotus* by Bradshaw (1962) and Bleier (1975); the right uterine horn is dominant. In all *Macrotus californicus* examined in the present study, this asymmetry was noted. Although several uteri from subadult individuals were symmetrical in shape, all adult uteri had hypertrophied right cornua. Uteri of *Micronycteris* and *Trachops* examined in this study were identical to pregnant and/or nonpregnant uteri of *Macrotus*.

In contrast to the *Macrotus*-group, the uteri of *Phyllostomus discolor, P. hastatus,* and *Phylloderma stenops* are externally simplex; these taxa are herein referred to as the *Phyllostomus*-group. Members of the *Phyllostomus*-group have externally simplex uteri with a tubular- to pear-shaped form (Fig. 4). The fundus of the uterus is prominent and rounded. The simplex uterus is regarded as the most highly derived external uterine anatomy among phyllostomoids.

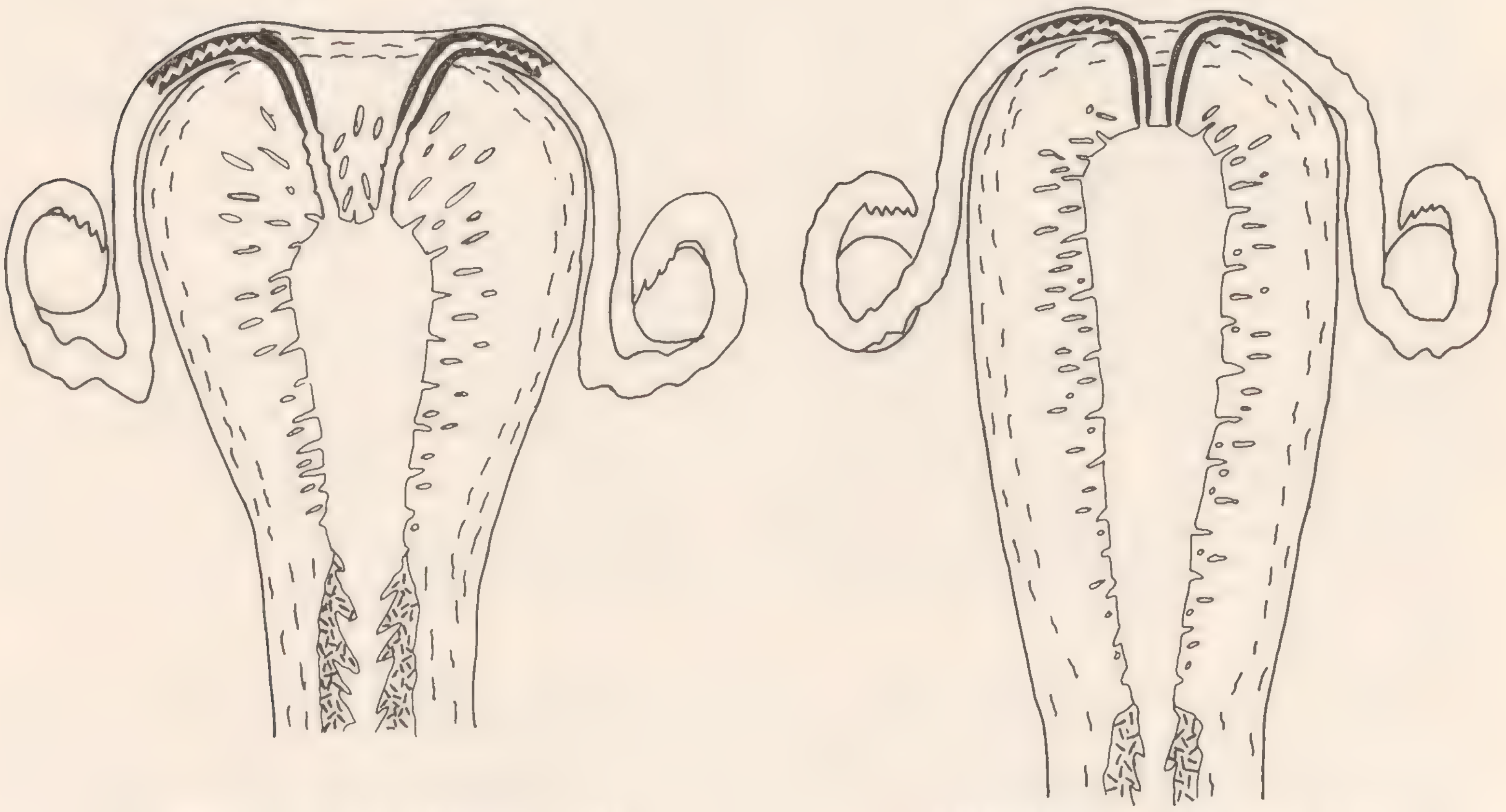
The internal uterine anatomy of the *Phyllostomus*-group consists of a large common lumen and narrow tubular segments. These tubular segments are actually extremely short uterine lumina and constitute the intramural uterine cornua (IUC; Fig. 4). In one specimen of *Phyllostomus discolor* we discovered an early-implanted blastocyst in an IUC (Fig. 5).

Virtually nothing is known concerning uterine histomorphology in *Phylloderma stenops* (Wilson, 1979). The uterus of one specimen examined in this study was reproductively inactive. Uterine histomorphology of this species was identical to *Phyllostomus*.

Subfamily Glossophaginae.—Bats of this subfamily are referred to as the long-tongued or long-nosed bats. As their name implies,



PHYLLOSTOMUS DISCOLOR PHYLLONYCTERIS APHYLLA



CAROLLIA PERSPICILLATA ARTIBEUS JAMAICENSIS

FIG. 4.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries in representative simplex phyllostomoids, including Phyllostominae: *Phyllostomus discolor*; Brachyphyllinae: *Phyllonycteris aphylla*; Carolliinae: *Carollia perspicullata*; Stenoderminae: *Artibeus jamaicensis*. The intramural uterine cornua (**iuc**) is a unique feature of the phyllostomoid simplex uterus. Abbreviations can be found in Fig. 1.

they have highly specialized, elongated muzzles. This subfamily consists of 13 genera and 32 species that live in the New World tropics and subtropics.

All members of this subfamily have externally simplex uteri (Fig. 5). Although some variation exists between genera, glosso-

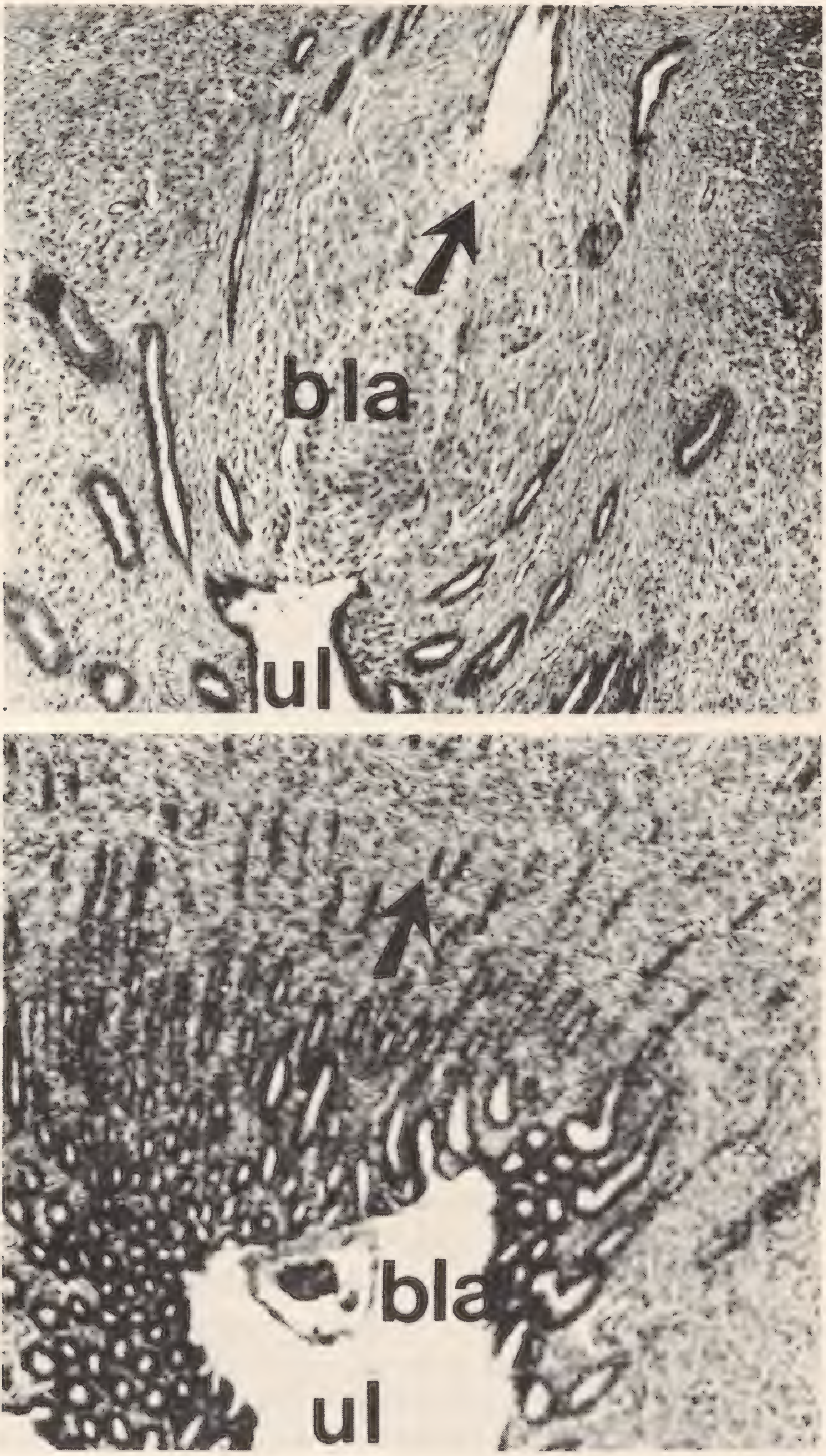


FIG. 5.—Initial sites of implantation and orientation of blastocysts in *Anoura geoffroyi* (*top*) and *Phyllostomus discolor* (*bottom*). In both specimens, blastocysts were implanted in the intramural uterine cornua and the inner cell mass was oriented towards the uterotubal junction of the oviduct ipsilateral to the developing corpus luteum. *Abbreviations:* **ul**, uterine lumen; **bla**, blastocyst; arrows in both photomicrographs indicate orientation towards the oviduct. Both 416×.

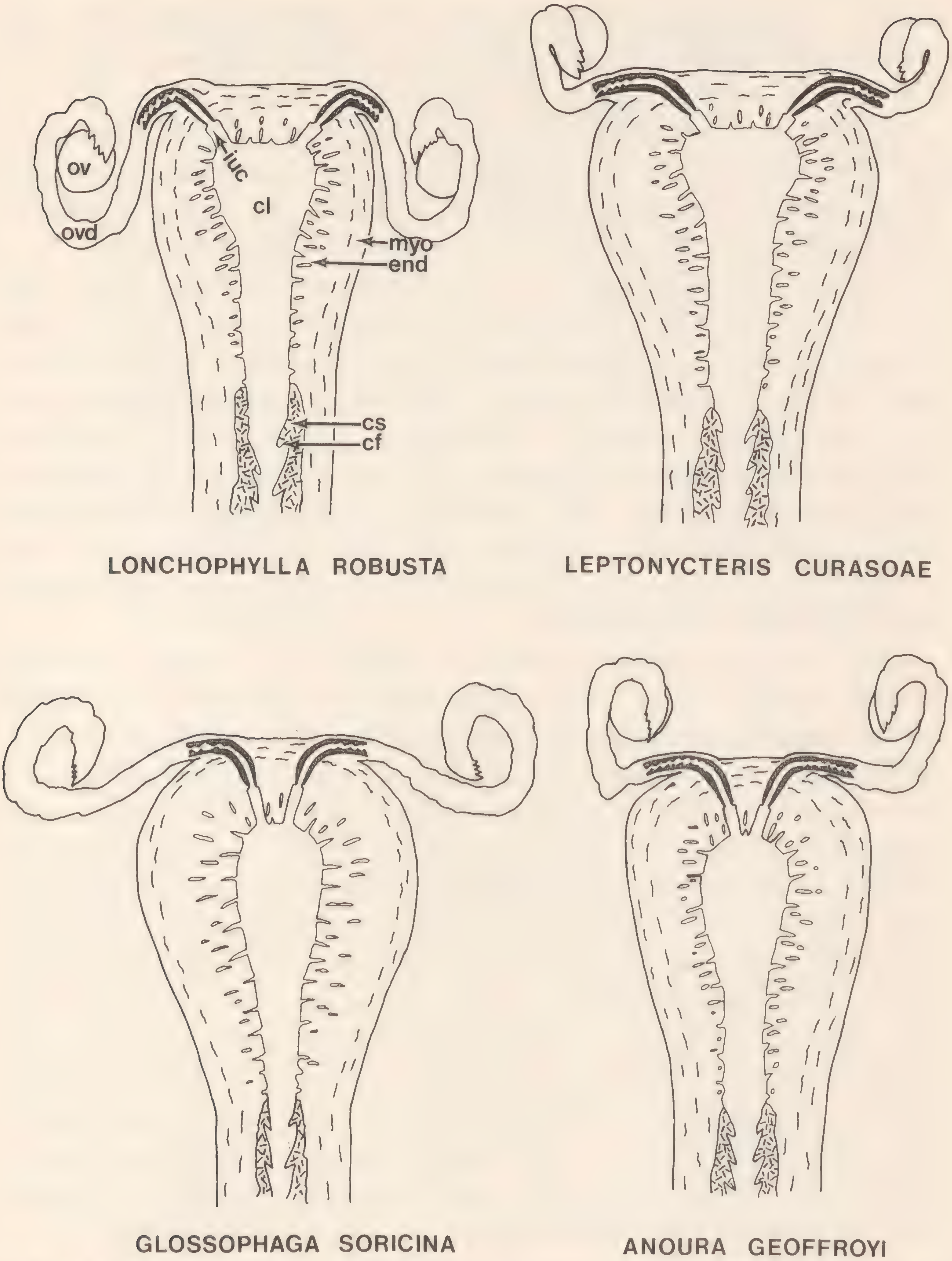
phagines have a distinctly barrel- to pear-shaped uterus. The fundus was notably flattened in all taxa examined. Internally, glossophagines have a large, common uterine lumen and tubular IUCs. The IUCs are short and broad in *Lonchophylla and Leptonycteris,* but longer in *Glossophaga, Monophyllus,* and *Anoura* (Fig. 6). Rasweiler (1974) has done extensive studies on the form and function of IUCs in *Glossophaga soricina* and noted that initial implantation always occurs in them. Likewise, we discovered an early-implanted blastocyst in an IUC of a specimen of *Anoura geoffroyi* (Fig. 5). Furthermore, in preovulatory specimens of *Leptonycteris* and *Monophyllus,* the endometrial lining of the IUCs was preferentially proliferating compared to that of the common lumen. These data suggest that IUCs function as the primary sites of implantation in all glossophagines.

Subfamily Brachyphyllinae.—This subfamily includes those bats referred to as the flower-bats. It contains three genera and seven species, all of which live in the West Indies. The systematics of this subfamily have been discussed by Baker and Bass (1979) (see Baker, 1979, for justification for using the name Brachyphyllinae rather than Phyllonycterinae). Uterine histomorphology in brachyphyllines agrees in all qualitative respects with that observed in the Glossophaginae (Figs. 4, 6). In both *Brachyphylla* and *Phyllonycteris* the uterus is externally simplex and barrel- to pear-shaped. The fundus is flattened and not prominent.

The internal uterine anatomy of *Phyllonycteris aphylla* includes a large, common lumen and short IUCs. These IUCs are oriented towards the latero-fundic border, an arrangement similar to that found in *Lonchophylla* and *Leptonycteris.* Although none of the *P. aphylla* examined had implanted blastocysts, all uteri had moderately to greatly proliferating endometrium lining the IUCs. These observations suggest that IUCs in *Phyllonycteris* function as in other phyllostomids with simplex uteri.

The one specimen of *Brachyphylla cavernarum* examined in this study possessed a large embryo. Unfortunately, invasion of embryonic tissues into the fundus of the uterus was so extensive that some uterine features could not be determined. Although IUCs were not observed, the oviducts descended from the latero-fundic border as in *Phyllonycteris.* Additional uteri of *Brachyphylla* could be profitably studied; presence of functional IUCs would be predicted based on their occurrence in *Phyllonycteris.*

Subfamily Carolliinae.— Bats of this subfamily are called short-tailed, leaf-nosed bats. These include two genera (*Carollia* and *Rhinophylla*) and eight species; all live in the Neotropics.



LONCHOPHYLLA ROBUSTA
LEPTONYCTERIS CURASOAE
GLOSSOPHAGA SORICINA
ANOURA GEOFFROYI

Fig. 6.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries in representative Glossophaginae, including *Lonchophylla robusta, Leptonycteris curasoae, Glossophaga soricina, Anoura geoffroyi*. Abbreviations can be found in Fig. 1.

Both *Carollia* and *Rhinophylla* have externally simplex uteri (Fig. 4). Bonilla and Rasweiler (1974) did extensive studies on uterine and oviductal histomorphology in *Carollia*. All species of *Carollia* examined in the present study had broadly pear-shaped uteri. The internal uterine anatomy includes a large, common lumen and long, tubular IUCs. We observed that blastocyst implantation occurs in the IUCs as in *Glossophaga soricina* (see also Bonilla and Rasweiler, 1974; Rasweiler, 1972, 1979*a*).

In contrast to *Carollia*, the uterus of *Rhinophylla pumilio* is less pear-shaped and more tubular in form. Internally, the uterus has a large, common lumen and short IUCs. No data were available regarding the function of IUCs as a site of implantation.

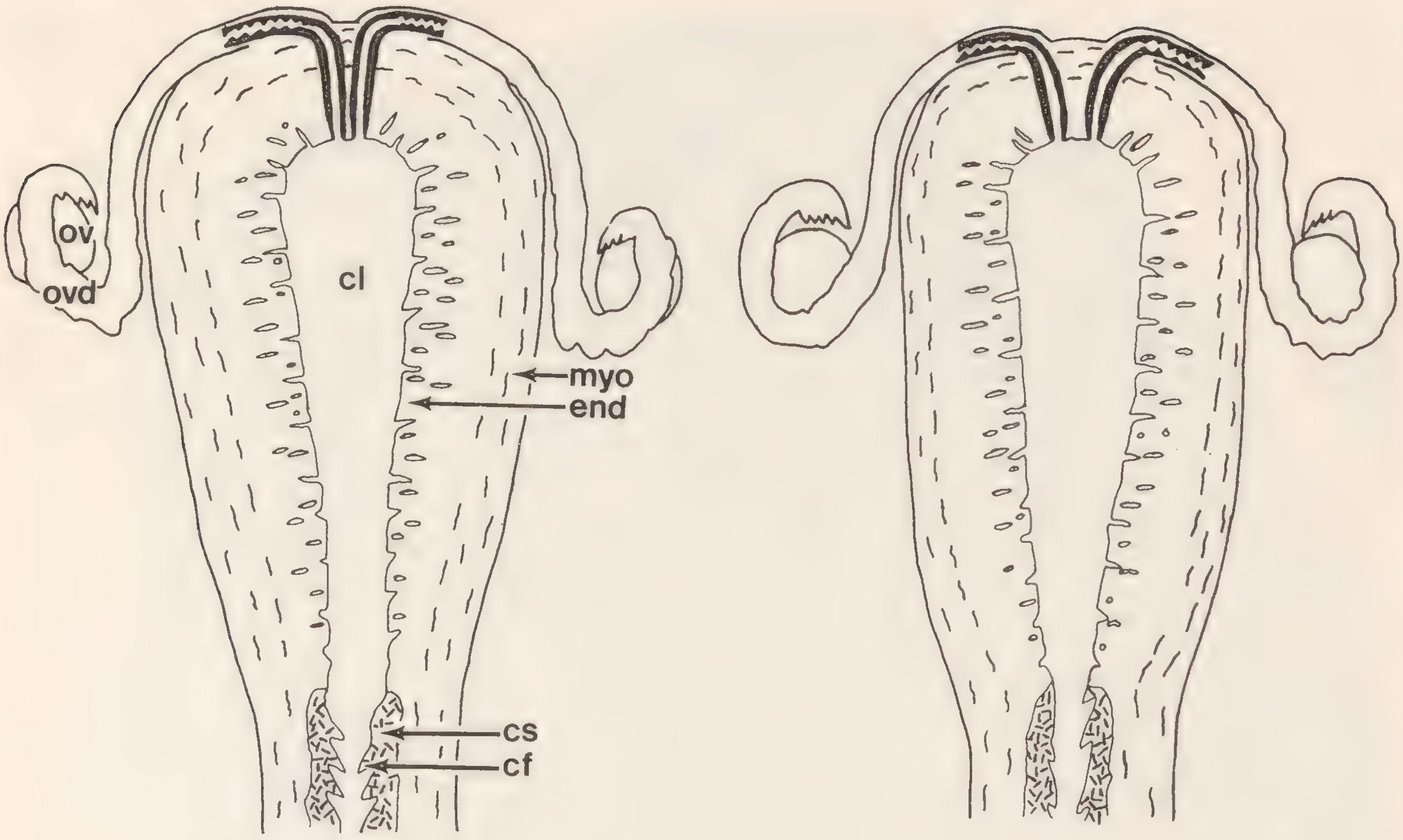
Subfamily Stenoderminae.—This subfamily includes those bats referred to as the New World fruit-eating bats. It includes 17 genera and 60 species. Although taxonomically diverse, stenodermines are a rather homogeneous group. Bats of the genus *Sturnira* have been considered a separate subfamily by some authors; however, recent workers regard this genus as a member of the Stenoderminae (Jones and Carter, 1976; Baker *et al.*, 1979). All stenodermines have distinctly tubular, simplex uteri (Figs. 4, 7). The fundic end of the uterus is covered by the oviducts which enter the uterine body near the midsaggital line.

The internal uterine anatomy consists of a single common lumen without IUCs. This simple internal anatomy is a unique feature of this subfamily and distinguishes the stenodermine uterus from all other simplex forms. The loss of IUCs is considered a continuation of uterine fusion involving the internal lumina and, as such, is considered a synapomorphy of the subfamily. In the absence of IUCs, blastocyst implantation must occur in the common lumen. It has been reported that implantation in *Artibeus jamaicensis* occurs in the fundic end of the common uterine lumen (Wislocki and Fawcett, 1941; Fleming, 1971). Likewise, we observed implantation in this region for all specimens that possessed blastocysts or embryos. These included two *Centurio senex*, one *Sturnira lilium*, one *Ectophylla alba*, and one *Ariteus flavescens* (Fig. 8). In all cases, the initial site of implantation was in the extreme fundic end of the uterine lumen (blastocyst orientation could not be determined except for *Ariteus*, see Fig. 8).

OVIDUCTAL HISTOMORPHOLOGY

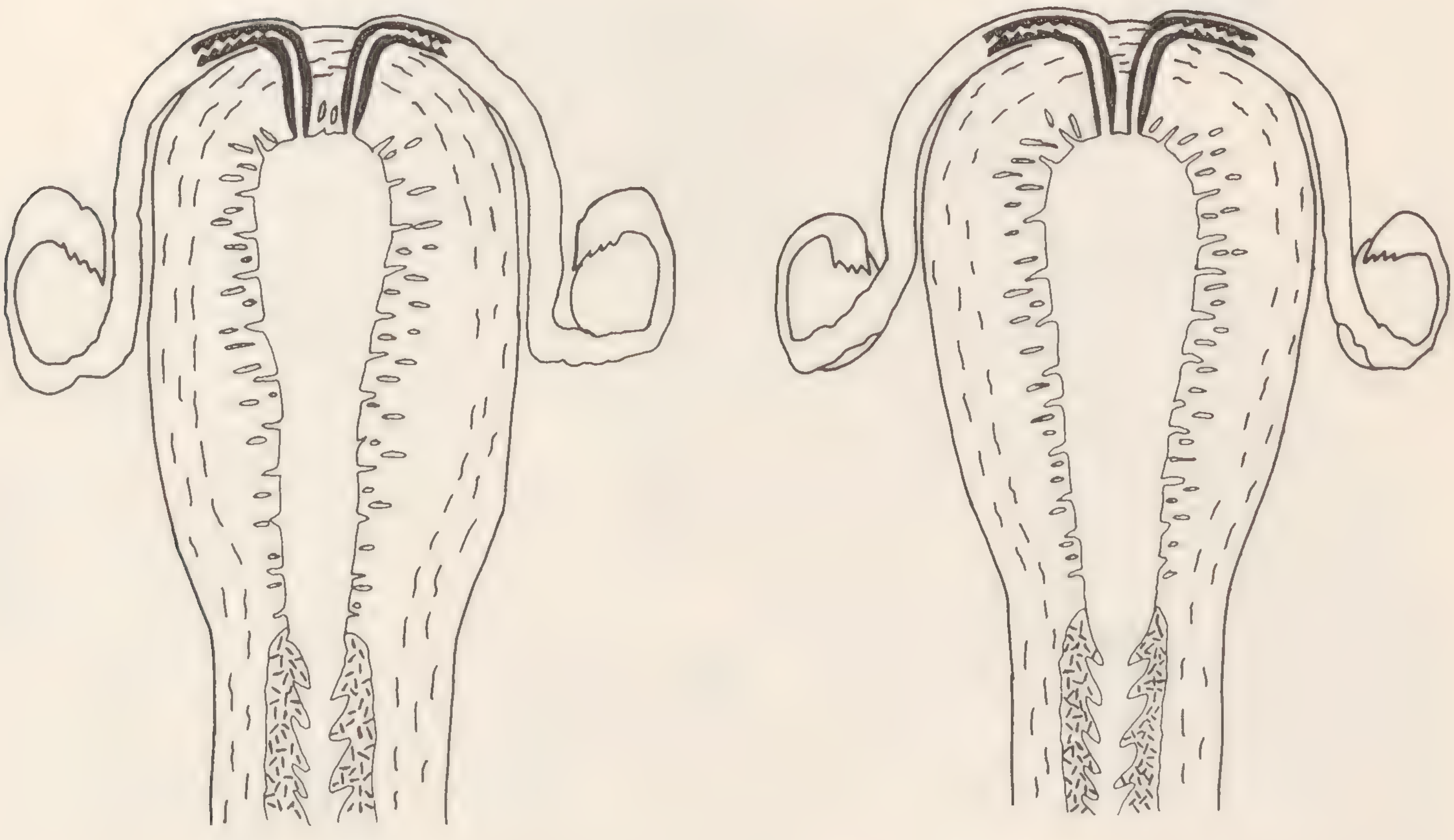
General Description

An excellent description of oviductal histomorphology can be found in Nilsson and Reinius (1969), whose terminology was followed in the present study. The oviduct is a tubular organ composed of three histologically well-defined tissue layers. An outer serosa is continuous with the peritoneum and joins the mesosalpinx to support the oviduct. A middle muscularis is comprised of



CENTURIO SENEX

URODERMA BILOBATUM



VAMPYROPS HELLERI

STURNIRA LILIUM

FIG. 7.—Semidiagramatic, frontal sections of the uterus, oviducts, and ovaries in representative Stenoderminae, including *Centurio senex*, *Uroderma bilobatum*, *Vampyrops helleri*, *Sturnira lilium*. Abbreviations can be found in Fig. 1.

circular and longitudinal smooth muscle layers and constitutes the bulk of the oviductal wall. The third and innermost tissue layer is a mucosa of simple to pseudostratified columnar epithelium with an underlying connective tissue (lamina propria). The oviductal epithelium undergoes marked histological changes dur-

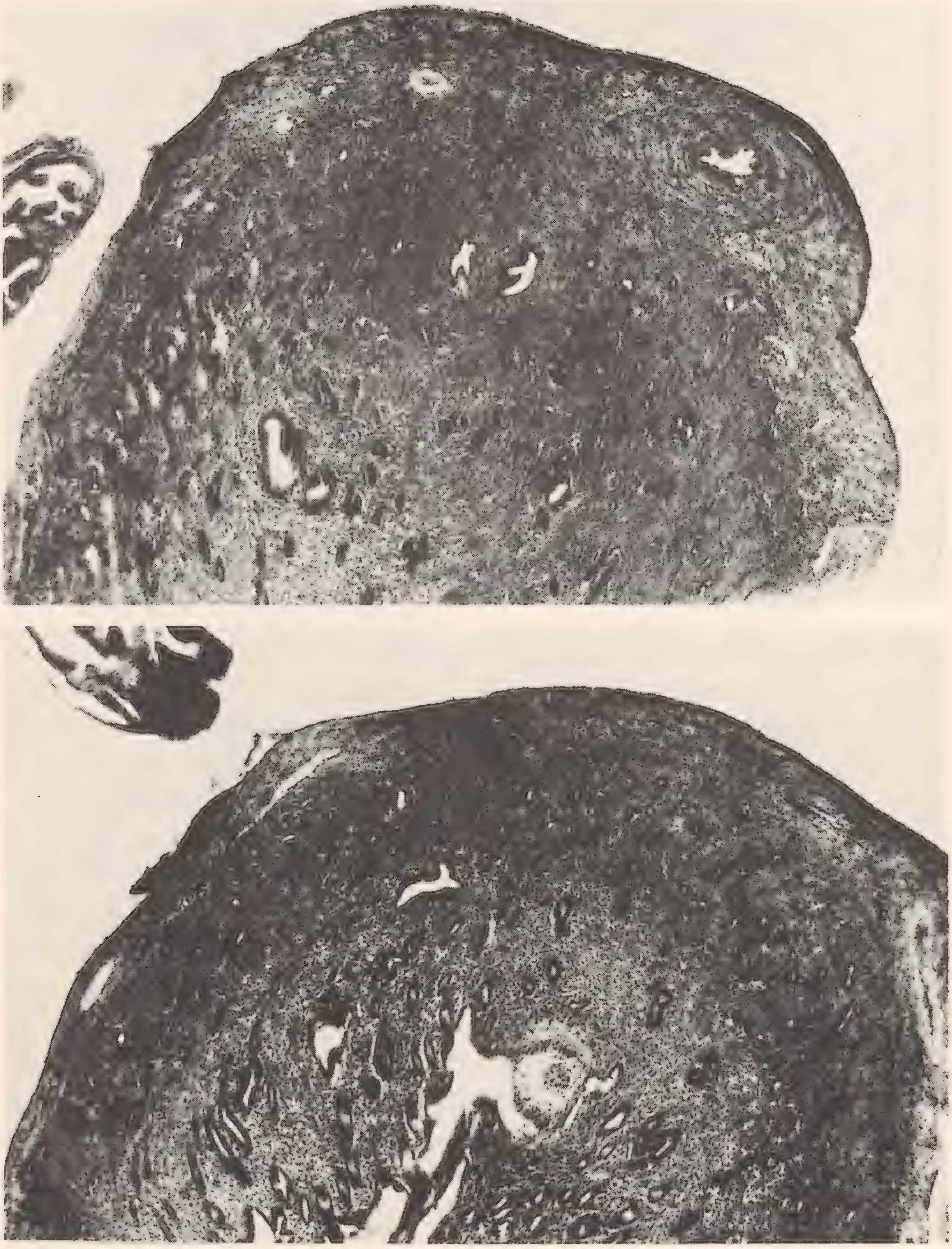


FIG. 8.—Photomicrographs of the uterus and oviducts of a specimen of *Ariteus flavescens* (serial sections viewed frontally). *Top:* Oviducts descend through the fundus on the midsaggital line. *Bottom*: several serial sections later, a blastocyst is found implanted in the fundic end of the common uterine lumen. Orientation of the inner cell mass was towards the oviduct ipsilateral to the developing corpus luteum. Both 50×.

ing the reproductive cycle. These changes include activation of secretory cells and development of cilia (Nilsson and Reinius, 1969). The lamina propria is heavily vascularized and acts as a structural framework for the epithelium. This organization is well illustrated as the mucosa is thrown into lamina propria-supported folds. These folds occur throughout the oviduct, but may vary in size or number in some regions (Nilsson and Reinius, 1969; this study).

The oviducts of phyllostomoid bats are coiled and regionally differentiated as in most eutherian mammals and all out-group chiropteran families examined. Beginning at the infundibular end, the oviductal regions include a preampulla, ampulla, isthmus, and junctura (Fig. 9). For the purposes of this study, these oviductal regions constitute the free portion of the oviduct and are defined herein as the extramural oviduct.

That portion of the oviduct that passes through the uterine wall is referred to as the intramural junctura (Nilsson and Reinius, 1969; Rasweiler, 1974). This oviductal region possesses all the histologically defined tissue layers found in the extramural oviduct, but lacks a definitive serosa. The muscularis is relatively thick and becomes continuous with the smooth muscle fibers of the myometrium. This portion of the oviduct has been the subject of considerable study because it involves the uterotubal junction (UTJ; Lisa *et al.*, 1954; Edgar and Asdell, 1960; Hafez, 1973*b*). The UTJ includes the intramural junctura and its opening into the uterine lumen (Hafez and Black, 1969). Although much of the research concerning the UTJ has been limited to domestic or laboratory mammals, available data suggest that this region has unique anatomical characteristics in some eutherian orders (Anderson, 1928; Lee, 1928; Hafez and Black, 1969).

The UTJ of bats has not been described in a comparative sense, although it has been discussed by several authors (Rasweiler, 1972, 1974; Karim, 1975; Mori and Uchida, 1980). Among the families and subfamilies of bats examined in the present study, the junction possesses considerable variation in form. In vespertilionids and molossids, the UTJ is a prominent colliculus, whereas it is a low papilla in rhinolophids, hipposiderids, and *Mystacina*, and a complicated, pocketed region in pteropodids and emballonurids (Fig. 1). In contrast, the UTJ in noctilionids, mormoopids, and phyllostomids has been markedly simplified. The lumen of the intramural junctura opens into the cornual lumen, IUC, or directly into the common uterine lumen without any oviductal or uterine elaboration (Figs. 2, 3, 4). The simple morphology of this region is regarded as a synapomorphy of the superfamily Phyllostomoidea. In the systematic accounts that follow, patterns of

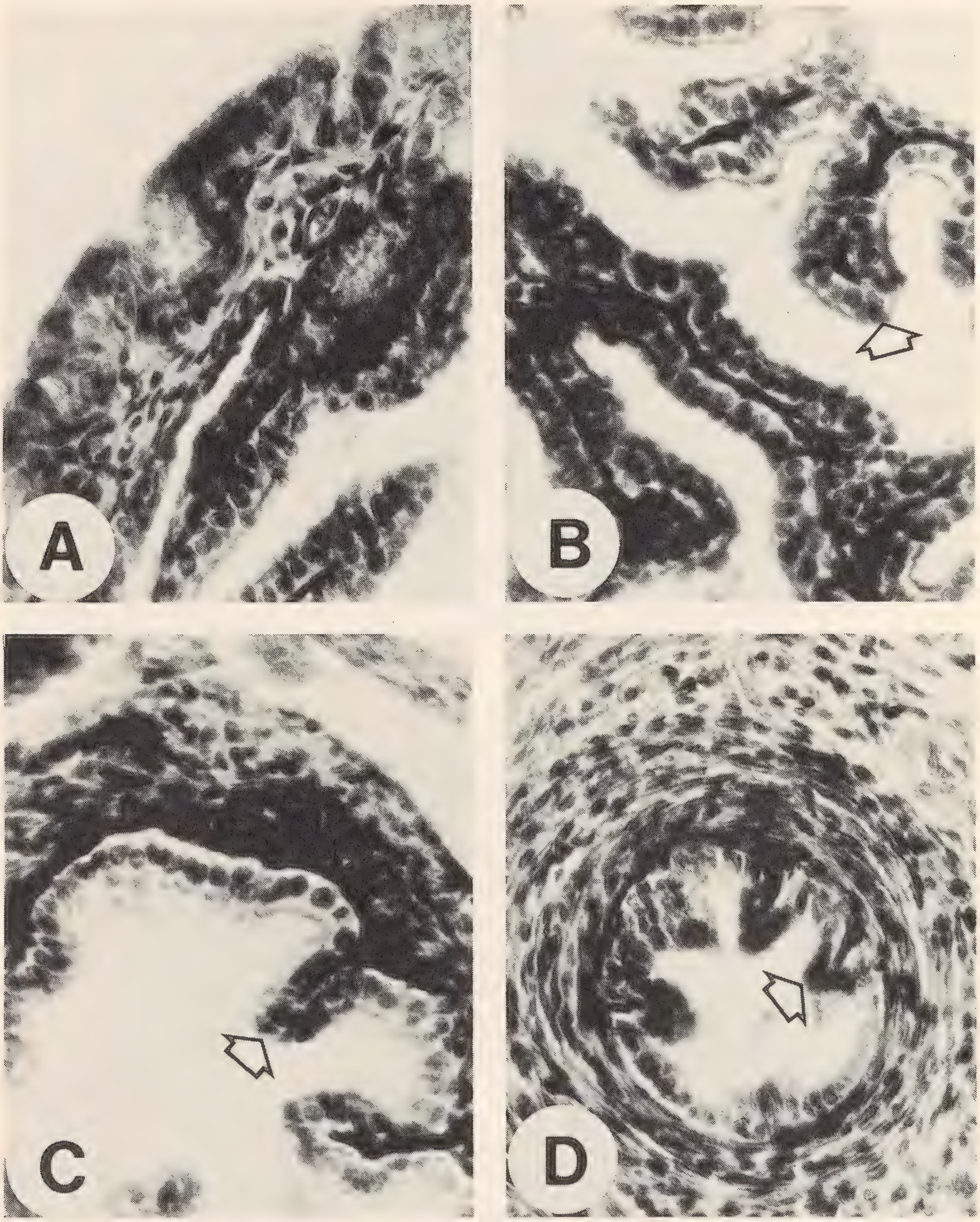


FIG. 9.—Oviductal histomorphology varies considerably among regions of the oviduct. This specimen of *Monophyllus redmani* was reproductively active, with a large corpus luteum but with no evidence of blastocyst or recent pregnancy. **A**, Preampulla with external folds (fimbriae) and high, cilliated epithelium; **B**, ampulla with prominent lamina propria-supported folds (arrow) and moderately high, cilliated epithelium; **C**, isthmus with relatively few, moderately low folds (arrow) but high, vacuolated epithelium; **D**, extramural junctura with narrow lumen and low folds (arrow) that usually lack lamina propria support and low, usually noncilliated epithelium. All photomicrographs 321×.

variation in oviductal histomorphology among phyllostomoid bats are illustrated and discussed.

Family Noctilionidae

Specimens of *Noctilio albiventris* and *N. leporinus* examined in this study possessed the same qualitative features of oviductal histomorphology. The oviduct of *N. albiventris* has been described in detail by Rasweiler (1977, 1978) and we confirm his observations.

The extramural oviducts enter the uterus at the apical tip of the cornua (Fig. 2). Just outside this entry the oviduct is reflected laterally, so that the extramural oviduct overlays the cranial end of the uterine cornua. This arrangement is similar to that observed in other bicornuate phyllostomoids and out-group chiropteran families (Figs. 1, 3).

The intramural junctura is a short segment which passes through the uterine wall and opens into the cornual lumen. A dense lamina propria supports prominent mucosal folds. These folds line the intramural junctura throughout its length to the UTJ (Figs. 3, 10). The UTJ is simple compared to the chiropteran out-groups examined; it opens into the cornual lumen without elaboration. However, it is perhaps noteworthy that the intramural junctura appears to empty into the internal cornual lumen somewhat below its apical tip (Fig. 3). This feature may represent a different mode of oviductal entry, or it may simply reflect the hypertrophied antimesometrial walls of the noctilionid uterus.

Rasweiler (1977, 1978) described a dramatic unilateral oviductal reaction in *Noctilio albiventris*. Under the influence of the active ovary, the ipsilateral oviduct is preferentially stimulated to secretory activity. The accumulation of glycogen and cytoplasmic vacuolation in oviductal epithelium may be controlled by local vascular pathways (Rasweiler, 1978). In the present study, specimens of *Noctilio albiventris* and *N. leporinus* that were preovulatory or with early-implanted blastocysts had hypertrophied, vacuolated oviductal epithelium. In all these specimens, branches of the ovarian and uterine arteries on the side ipsilateral to the active ovary were prominent and blood-engorged.

Family Mormoopidae

The oviducts of *Pteronotus* and *Mormoops* are short, highly coiled, and regionally differentiated. Entry of the extramural ovi-

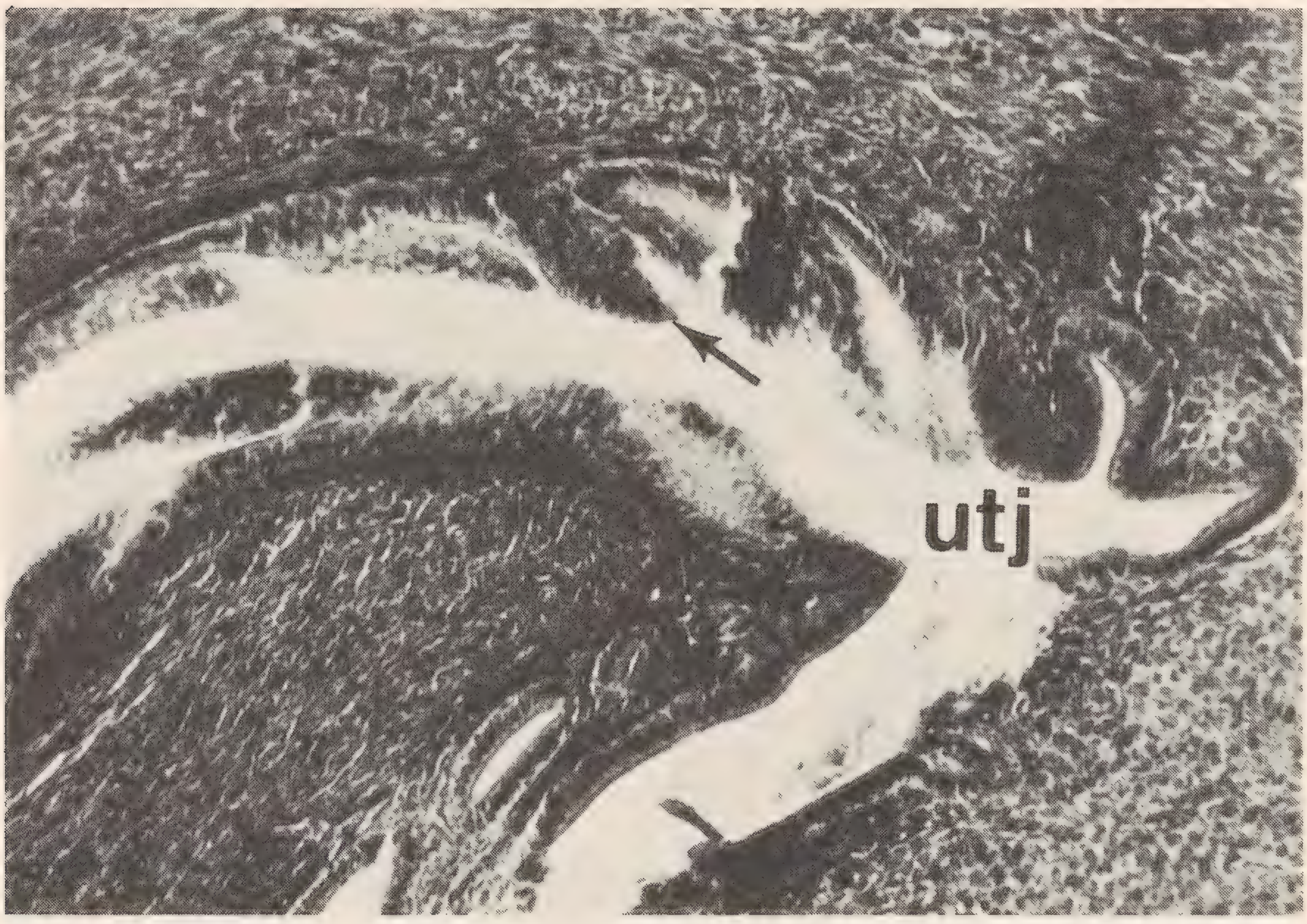


FIG. 10.—Photomicrograph of the intramural oviduct and uterotubal junction (**utj**) of *Noctilio leporinus* (frontal section). The oviductal mucosa has lamina propria-supported folds throughout the intramural junctura (see arrow). 279×.

duct occurs at the apical tip of the cornua as in other bicornuate phyllostomoids (Fig. 3). As in *Noctilio,* the extramural oviduct is reflected laterally, covering part of the cranial end of the uterine cornua.

The intramural junctura is a short oviductal segment that passes through the uterine wall and opens into the cornual lumen. At the UTJ, the oviductal lumen clearly opens at the extreme apical tip of the internal cornual lumen, an arrangement unlike that observed in noctilionids, but similar to that of *Desmodus* and the *Macrotus*-group. Mucosal folds are prominent throughout the intramural junctura and are supported by a dense lamina propria.

Available data on mormoopid reproductive physiology suggest that these bats are entirely right side dominant (Wimsatt, 1979). All specimens examined in this study confirmed this. In two specimens of *Pteronotus parnellii* that possessed early-implanted blastocysts, the right oviduct was preferentially hypertrophied. However, in nonpregnant, preovulatory specimens of *P. quadridens* and *P. macleayii,* both oviducts exhibited secretory ability. In addition, branches of ovarian and uterine arteries and veins were seen to course between the ovaries and uterus in specimens of all these taxa (Fig. 11).

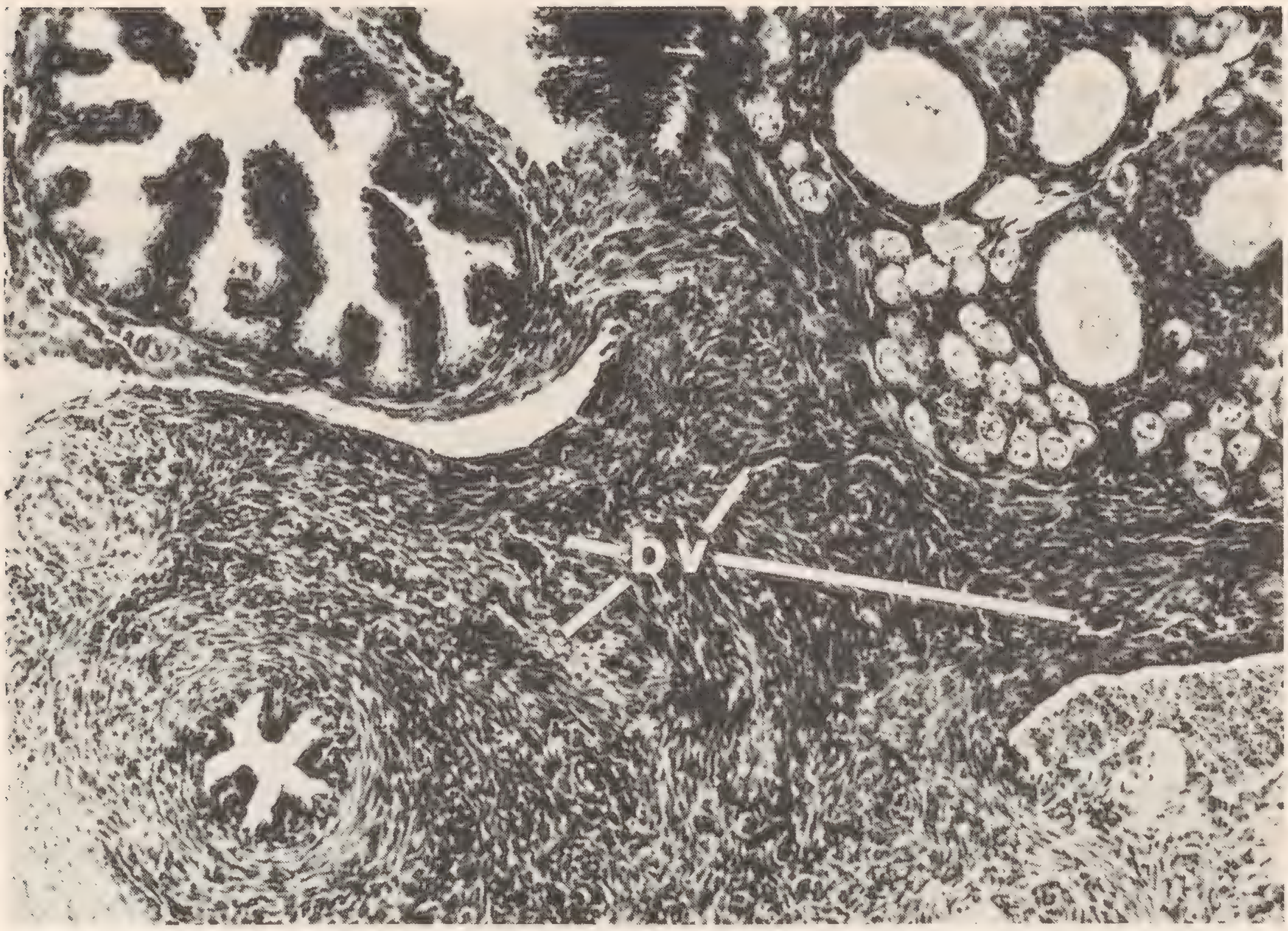


FIG. 11.—Photomicrograph illustrating uterine-ovarian relationships in a specimen of *Pteronotus macleayi.* Blood vessels (**bv**) were found between the active right ovary and the cranial end of the right uterine cornu. 378×.

Family Phyllostomidae

Recent studies have detailed oviductal histomorphology in several phyllostomids, including *Desmodus, Glossophaga,* and *Carollia* (Rasweiler, 1972, 1974; Bonilla and Rasweiler, 1974; Quintero and Rasweiler, 1974). These studies suggest that phyllostomids share features of oviductal histomorphology with noctilionids and mormoopids.

Anatomical relationships between the uterus and extramural oviduct were found to be quite variable among phyllostomids. In those taxa that possess bicornuate uteri (i.e., *Desmodus* and the *Macrotus*-group), the extramural oviduct contacts and enters the apical tip of the cornua, an arrangement like that found in noctilionids and mormoopids (Fig. 3). On the other hand, phyllostomids with simplex uteri have a number of distinct forms of oviductal entry. In the *Phyllostomus*-group, the oviducts enter the uterine body on the lateral (mesometrial) border (Fig. 4), whereas oviducts in all other simplex forms enter on the fundic border (Figs. 4, 6). This fundic pattern of external entry shows considerable variation among phyllostomid subfamilies. The site of entry in glossophagines, brachyphyllines, and carolliines is more lateral than in stenodermines.

Although the extramural oviducts contact and enter the uterus on the fundic border in glossophagines, the site of entry is somewhat variable (Fig. 6). In *Lonchophylla* and *Leptonycteris*, the external entry is on the latero-fundic border of the uterus. On the other hand, the entry in *Glossophaga, Monophyllus,* and *Anoura* is more towards the midline. In all glossophagines examined in this study, the intramural juncturae pass through the uterine wall and open into the IUCs. Due to the more lateral site of entry in *Lonchophylla* and *Leptonycteris*, the juncturae in those taxa are far apart with a large mass of functional uterine tissue between the oviducts. In *Glossophaga, Monophyllus,* and *Anoura,* the more fundic site of entry allows the intramural juncturae to converge on the midline. As a result, a smaller amount of functional tissue is interposed between the oviducts. Features of oviductal histomorphology in brachyphyllines agree in all qualitative respects with those observed in glossophagines. The site of entry in both *Phyllonycteris* and *Brachyphylla* is on the latero-fundic border of the uterus. This site of entry is identical to that of *Lonchophylla* and *Leptonycteris* (Figs. 4, 6).

Both *Carollia* and *Rhinophylla* have extremely long, coiled oviducts. The external entry of the extramural oviducts in *Carollia* occurs on the latero-fundic border of the uterus, a site of entry similar to that illustrated in *Glossophaga* (Fig. 4). However, in *Rhinophylla,* the external entry is more towards the midline, thus similar to that observed in *Anoura.* The extramural oviducts of both genera turn laterally and travel along the fundic border of the uterus. Upon reaching the mesometrial border they descend along the sides of the uterine body where they encircle the ovaries. This arrangement is similar to that found in stenodermines. The intramural juncturae of both *Carollia* and *Rhinophylla* converge on the midline where they open into the IUCs. The site of external entry and pathways of intramural juncturae result in relatively little functional uterine tissue being found between the oviducts.

Oviducts of all stenodermines examined in this study were long and tortuously coiled. Although the external entry of the extramural oviduct varies to some degree among stenodermine taxa, the entry is very near the midsaggital line in all members of this subfamily. In some taxa (e.g., *Uroderma, Vampyrops, Vampyressa, Vampyrodes,* and *Ariteus*), the site of entry is well off the midline; in others (e.g., *Artibeus, Enchisthenes, Sturnira,* and *Ectophylla*) the site is closer to the midline. In the most extreme cases (*Centurio* and *Ametrida*) the oviducts enter on the midline (Figs. 4, 5, 7, 12). As a result of a fundic external entry and the pathway of intramural juncturae, little uterine tissue is interposed between the oviducts. Functional endometrium was lacking in this region in all but two taxa (*Vampyrops helleri* and *Vampyressa pusilla*). In all other stenodermines, the interposing uterine tissue is limited to a dense connective tissue stroma.

Resolution of the primitive or derived nature of the lateral and fundic oviductal entries in phyllostomids with simplex uteri is not simple. There are no ontogenetic data available on the development of the phyllostomid simplex uterus, and out-group comparison cannot be readily applied to determine the polarity of this phylogenetic character. However, based on indirect evidence of comparative and ontogenetic studies of the simplex uterus in anthropoid primates and edentates, it appears that a lateral entry is most easily derived from a bicornuate uterine anatomy. In the absence of contradictory evidence, we propose that a lateral entry, as exemplified by the *Phyllostomus*-group, is primitive for simplex phyllostomids. With progressive uterine fusion, the oviductal junction moves towards the midsaggital line with the result that the fundic entry of glossophagines, brachyphyllines, and carolliines is regarded as a derived morphology. This progressive movement of the oviductal entry reaches its most highly derived form in stenodermines.

The phyllostomid intramural oviduct possesses several unique features. Mucosal folds, prominent in the intramural junctura of noctilionids and mormoopids, were notably reduced in all phyllostomids examined (Fig. 13). This reduction of mucosal folds begins in the extramural oviduct near the external entry and continues to the UTJ. The mucosal lining of some taxa shows low folds, but these are without a supporting lamina propria. Restriction of mucosal folds to the extramural oviduct is a unique feature among bats and is considered a synapomorphy of the family.

Unilateral oviductal reactions have been described in *Glossophaga*, *Carollia*, and *Desmodus* (Rasweiler, 1972; Bonilla and Rasweiler, 1974; Quintero and Rasweiler, 1974). In this study, these reactions also were observed in the oviducts of preovulatory and early-pregnant specimens of these taxa. Identical unilateral reactions (ipsilateral to the functional corpus luteum) were observed in preovulatory and early-pregnant specimens of the following phyllostomid taxa: *Phyllostomus discolor*, *P. hastatus*, *Monophyllus redmani*, *Leptonycteris curasoae*, *Phyllonycteris*

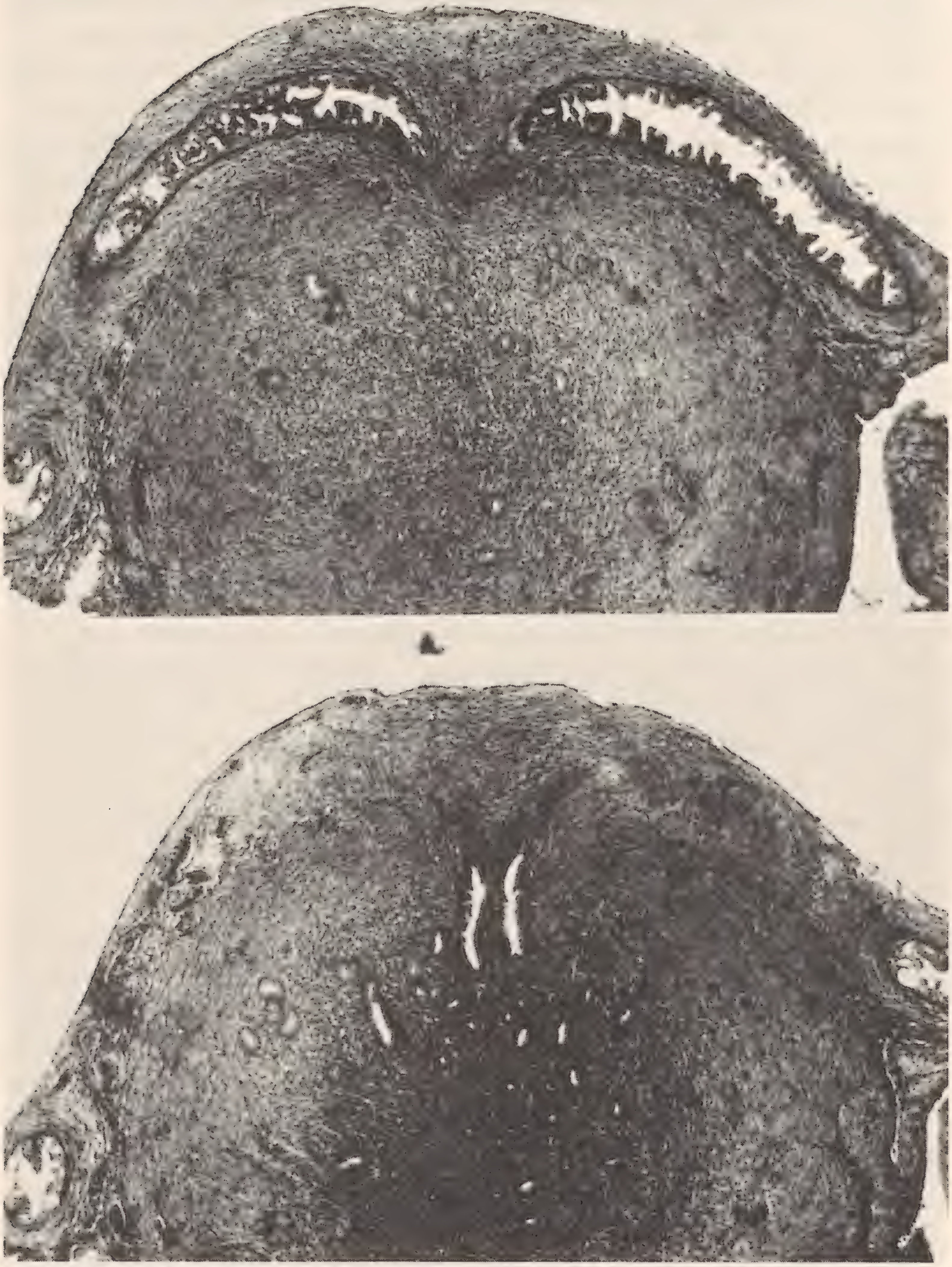


FIG. 12.—Photomicrographs of the uterus and oviducts of a specimen of *Sturnira lilium* (serial sections viewed frontally). *Top:* Extramural oviducts overlay the fundic end of the uterus before they descend on the midsaggital line. *Bottom:* This photomicrograph, taken several sections later, illustrates the descent of the intramural juncturae on the midsaggital line. Both 64×.

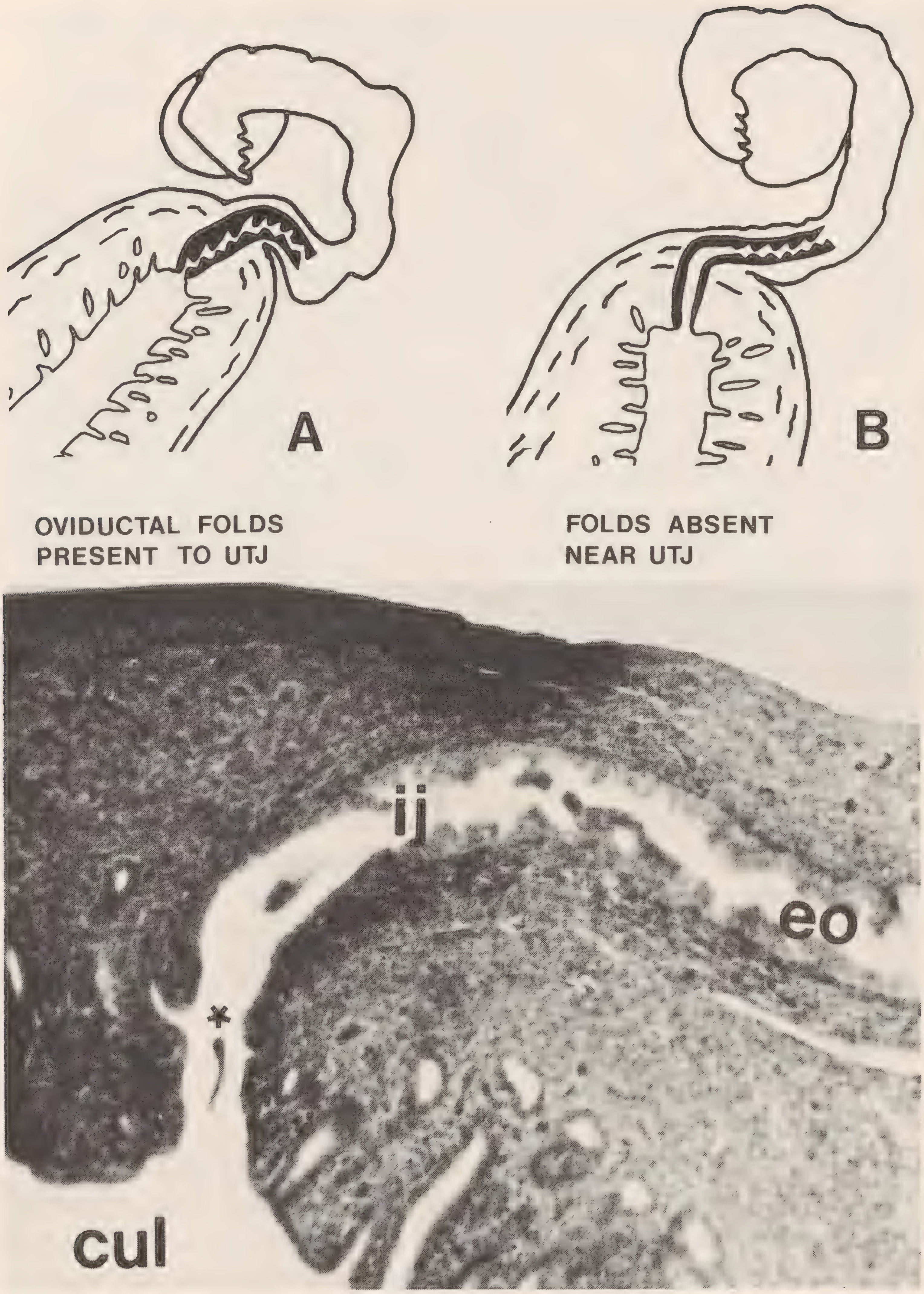


FIG. 13.—*Top:* Diagram to illustrate oviductal mucosal fold character: **A**, mucosal folds present throughout oviduct to the uterotubal junction, as in noctilionids and mormoopids; **B**, folds lacking in the intramural junctura, as in phyllostomids. *Bottom*: Photomicrograph of the oviduct and uterus of *Glossophaga soricina* (frontal section). The oviductal mucosal folds are restricted to the extramural oviduct as in **B**, above. *Abbreviations:* **cul**, common uterine lumen; **ij**, intramural junctura; **eo**, extramural oviduct; asterisk indicates position of the intramural uterine cornu. 98×.

aphylla, *Ariteus flavescens*, *Artibeus jamaicensis*, and *Sturnira lilium*.

OVARIAN HISTOMORPHOLOGY

Little is known concerning the comparative morphology of the ovary in phyllostomoid bats (Mossman and Duke, 1973). Rasweiler (1972) briefly commented on the ovaries of *Glossophaga soricina*. Likewise, Bonilla and Rasweiler (1974) noted interstitial tissues in *Carollia*. The most comprehensive study on ovarian morphology and histology of a phyllostomid was given by Wimsatt and Trapido (1952) for *Desmodus*. Ovaries of phyllostomoid bats examined in the present study were generally ellipsoidal to spherical in shape. Notable exceptions included mormoopids and the *Macrotus*-group, which have markedly flattened, atrophic left ovaries. In addition, both specimens of *Leptonycteris curasoae* had distinctly kidney-shaped ovaries.

Ovarian histomorphology in phyllostomoid bats is typical by eutherian standards. A cortex and medulla were readily identified in all phyllostomoids examined; the cortex contained primary follicles and a dense connective tissue stroma, whereas the medulla contained maturing follicles, corpora lutea, and numerous blood vessels. In most phyllostomoids, primary follicles are distributed throughout the cortex. However, in *Glossophaga soricina* and *Leptonycteris curasoae*, these follicle types are limited to the medial and lateral aspects of the ovary, respectively. It has been noted that polyovular follicles occur relatively rarely within mammals (Mossman and Duke, 1973; Harrison and Weir, 1977). In the present study, one young, nonpregnant specimen of *Ametrida centurio* was found to possess numerous polyovular follicles in both ovaries (Fig. 14).

Interstitial tissues are diverse; thecal and gonadal adrenal types were present in all taxa examined. In some taxa (e.g., *Carollia*) massive amounts of gonadal adrenal interstitial tissue were found in the mesovarium and ovarian hilus, observations identical to those reported by Bonilla and Rasweiler (1974). Mossman and Duke (1973:209) noted an unusual rete-type interstitial tissue in *Uroderma*. In the two specimens of *Uroderma* examined in this study, the rete epithelium was not active; however, several specimens of *Phyllonycteris* and *Carollia* did have hypertrophied rete epithelium.

The ovary and oviduct are generally suspended by the mesovarium and mesosalpinx which together form the ovarian bursa.

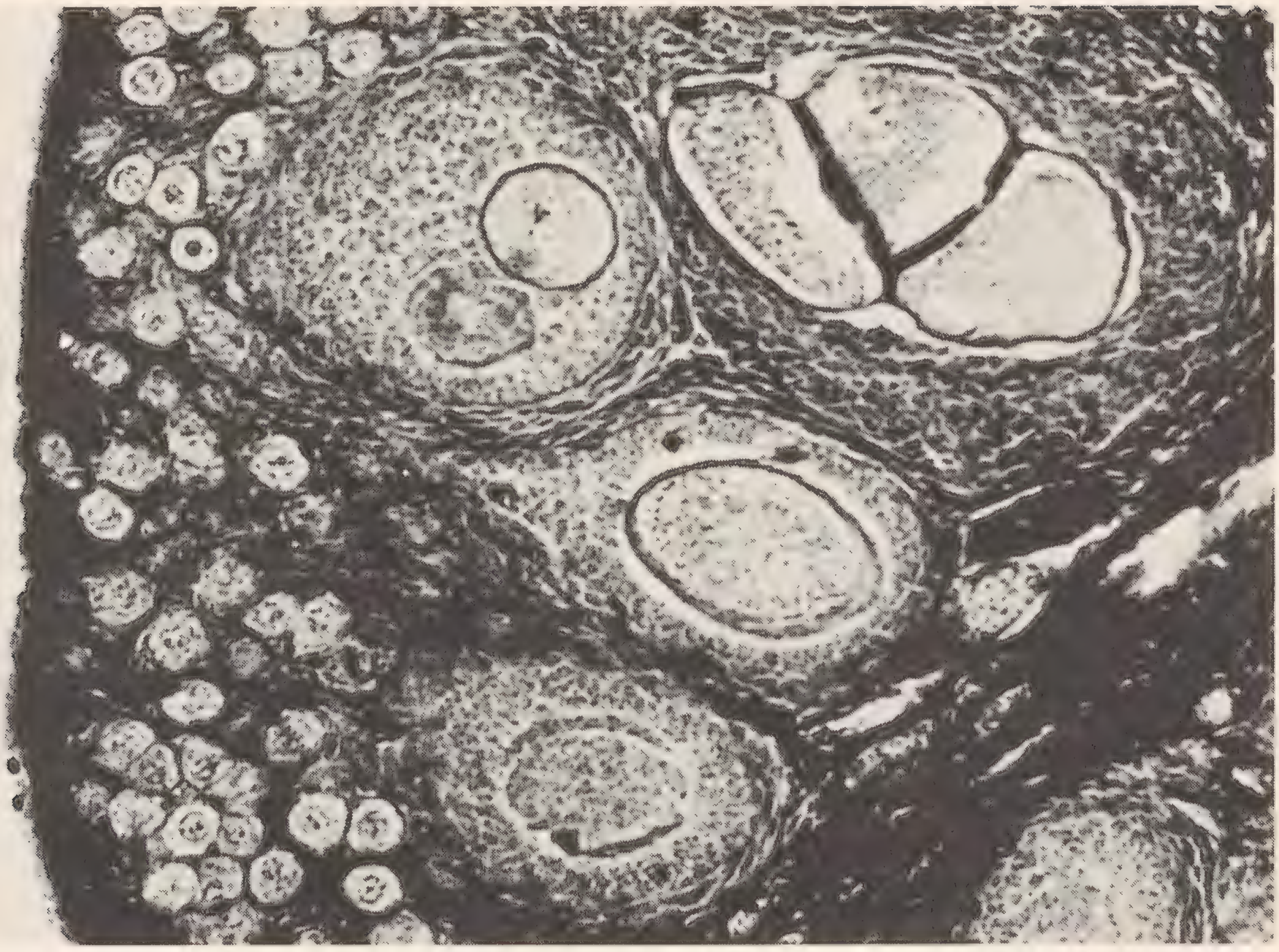


FIG. 14.—Polyovular follicles were found in both ovaries of a specimen of *Ametrida centurio*; these ranged in extent of development from small secondary to moderately large vesicular follicles. 240×.

Surprisingly, noctilionids, mormoopids, and phyllostomids possess a complex array of bursal arrangements. We will briefly summarize the bursal types observed among these families using the terminology of Mossman and Duke (1973). A partial bursal type with a laterally recurved oviduct and a medium to large peritoneal opening was found in Mormoopidae, *Phyllostomus*-group, Brachyphyllinae, and Glossophaginae (exclusive of *Anoura* and *Lonchophylla*; see below). As a variation, partial bursae with a medially recurved oviduct and a medium to large slitlike peritoneal opening were found in the *Macrotus*-group, *Desmodus*, and *Anoura.* On the other hand, a complete bursa with a medially recurved oviduct and a minute porelike or small slitlike opening was noted in *Lonchophylla*, Carolliinae, and Stenoderminae. *Noctilio* also possessed a complete bursa, but there the oviduct wrapped around the cranial end of the ovary.

The ovarian ligament extends from the ovary to an attachment at the junction of the oviduct and uterus. Comparative and ontogenetic studies have shown that this arrangement is a rather constant feature among eutherian mammals (Mossman, 1977). In the present study, this attachment was observed in all phyllostomoids except the Carolliinae and Stenoderminae (Fig. 15A). In these phyllostomid subfamilies the ovarian ligament does not attach in this manner, but is attached to the lateral (mesometrial) border of the uterus (Fig. 15B). This arrangement is quite independent of the mesenteries that generally suspend the reproductive organs. This modified site of ligamentous attachment is an apparently unique feature among mammals and therefore is considered to be a synapomorphy of these two subfamilies.

Discussion

Histomorphological features of the uterus, oviducts, and ovaries in the New World bat families Noctilionidae, Mormoopidae, and Phyllostomidae illustrate a pattern of synapomorphy suggesting that phyllostomoid bats share a common evolutionary history. It is striking that extensive evolution of uterine morphology has occurred in these closely related families, compared to the conservatism found in most eutherian orders (Robin, 1881; Wood Jones, 1917; Matthews, 1941; Mossman, 1977). Comparative anatomists and embryologists have generally accepted a "fusion hypothesis" for the evolution of uterine morphology. This hypothesis is based on morphological and ontogenetic data viewed from a framework of out-group comparison. The present study has documented histomorphological details of the female reproductive tract in 29 genera and 36 species of phyllostomoid bats. Derived character states were hypothesized using out-group comparison. Phylogenetic relationships based on a cladistical analysis of the data presented in this paper are discussed by Hood and Smith (1982).

Wimsatt (1975, 1979) and Mossman (1977) have discussed at length some features of reproductive biology that apparently are correlated with uterine morphology. The most consistent correlation is found in litter size; mammals with short bicornuate and simplex uteri carry only one or a few young. However, bats represent a major exception to this correlation. The majority of chiropteran species, including those with duplex and long bicornuate uteri, produce and carry but a single fetus (cases of twinning are known for several families). Available data on noctilionids, mormoopids, and phyllostomids suggest that these three families are generally monovular and monotocous (Anderson and Wimsatt, 1963; Rasweiler, 1977; Bleier, 1979; Wilson, 1979). It seems clear, then, that the diversification of uterine morphology in phyllostomoid bats, and in the order Chiroptera as a whole, is not simply explained by adaptation towards small litter size.

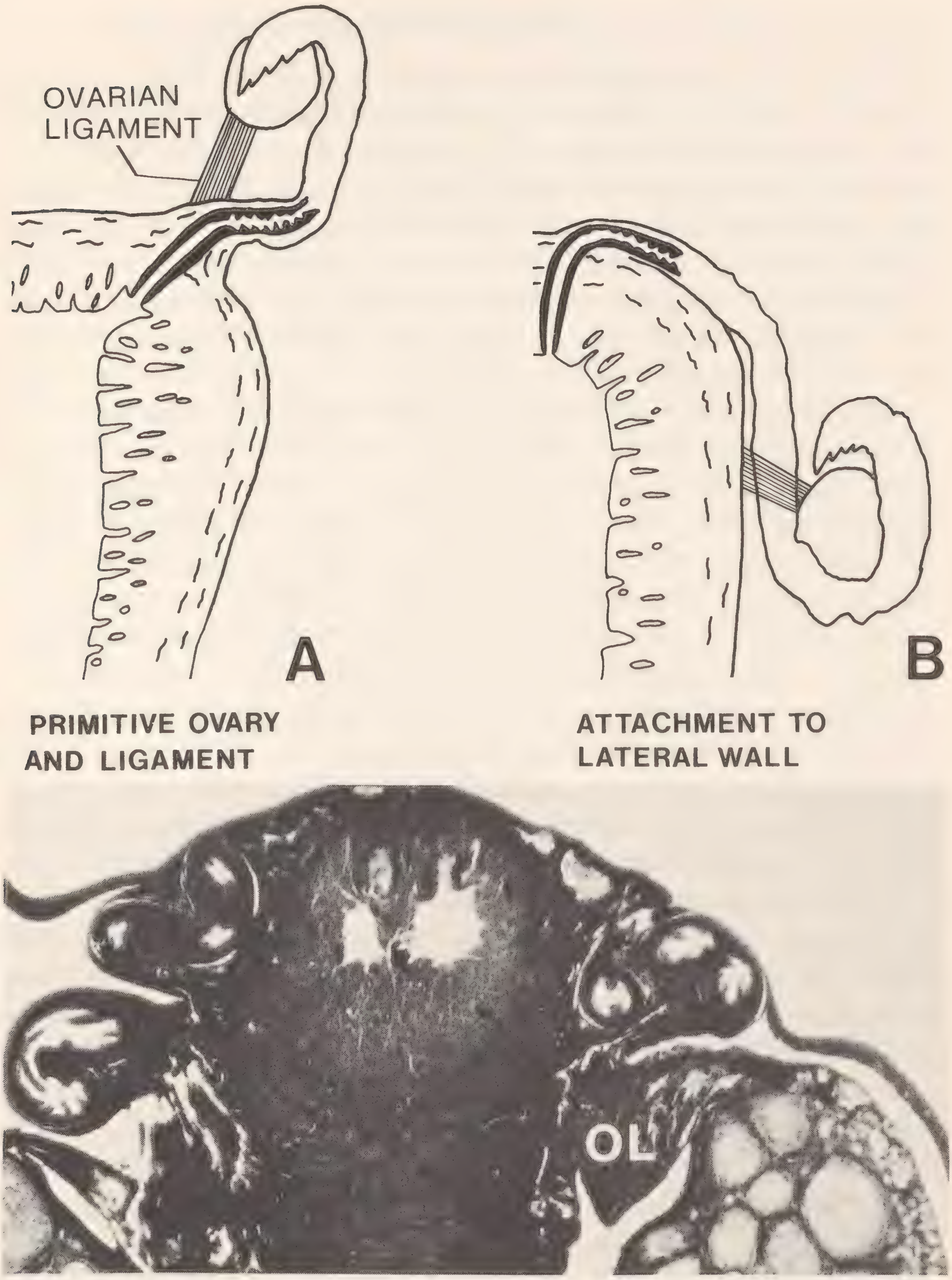


FIG. 15.—*Top*: Diagram to illustrate the ovarian ligament character: **A**, normal attachment between ovary and external entry of oviduct, as found in most eutherian mammals; **B**, modified attachment site, as found in carolliines and stenodermines. *Bottom*, Frontal section of the uterus, oviduct, and ovaries of *Vampyrops helleri*. The ovarian ligament (**ol**) extends from the ovary to an attachment site on the lateral (mesometrial) border of the uterus as in **B**, above. 40×.

Reproductive Asymmetry and Unilateral Reactions

Anatomical and physiological asymmetry is not known to be a major reproductive feature in eutherian mammals. However, in bats asymmetry dominates the reproductive strategies of several families (Wimsatt, 1979). Within phyllostomoid bats, mormoopids and the *Macrotus*-group are markedly asymmetrical (with right-side dominance). Details of mormoopid reproduction are virtually unknown and need to be examined. In the two *Pteronotus parnellii* that had early-implanted blastocysts, implantation occurred in the right horn and the corpus luteum was found in the right ovary. In contrast, a number of studies have been conducted on asymmetry in *Macrotus californicus,* which have shown that only the right ovary ovulates and the blastocyst always implants in the right uterine horn (Bradshaw, 1962; Bodley, 1974; Bleier, 1975). However, Bleier and Ehteshami (1981) demonstrated that when the right ovary is surgically removed, the left ovary can ovulate with subsequent development of early-implanted blastocysts in the left horn. These data suggest that expression of ovarian capacitance is complex and may be controlled by a number of factors. In the present study, the phyllostomine genera *Micronycteris* and *Trachops* have uterine morphologies similar to *Macrotus.* However, none of these specimens were preovulatory or pregnant; therefore, details of the reproductive cycle are unknown.

Unilateral oviductal and uterine reactions are known to occur in *Noctilio* and several phyllostomid genera (Rasweiler, 1978; 1979*a*). However, unilateral reactions are not unique to those families, but have been recorded in several species of Pteropodidae and Emballonuridae (Marshall, 1953; Gopalakrishna and Murthy, 1960; Gopalakrishna and Karim, 1971). Rasweiler (1978, 1979*a*) has hypothesized that local veno-arterial pathways mediate these reactions and that unilateral oviductal reactions are important in the prolonged oviductal development of preimplanted blastocysts. We observed unilateral oviductal reactions in our specimens of *Noctilio, Pteronotus parnellii* (but not in other mormoopids), and in several phyllostomids. Local uterine-ovarian vascular systems were observed histologically in all noctilionid and mormoopid taxa examined. The function of these remains unverified. Further studies on reproductive physiology in phyllostomoid bats would certainly benefit our general understanding of reproductive asymmetry in bats.

Implantation

The process of blastocyst implantation has been reviewed by Wimsatt (1975) and discussed by Rasweiler (1979*a*). Sites of implantation are quite variable in bats. Initial implantation may occur anywhere in the gestational uterus of many taxa, although some bats have a restricted site of implantation at the cranial end of the uterine cornua (Rasweiler, 1979*a*). Among bicornuate phyllostomoids, blastocysts of *Noctilio* initially implant at the cranial end of the uterine cornua. In simplex forms, the intramural uterine cornua (IUCs) are further restricted sites. We confirmed these observations in our specimens of *Noctilio* and several phyllostomids and newly documented the function of IUCs in *Phyllostomus* and *Anoura.* On the basis of our histological observations (hypertrophied endometrium), IUCs can serve as primary sites of implantation in glossophagines, brachyphyllines, and carolliines. In stenodermines (which lack IUCs), blastocysts implant at the extreme fundic end of the common uterine lumen.

Orientation of the embryonic mass of the blastocyst at initial implantation is extremely variable in bats. In *Macrotus, Glossophaga,* and *Carollia* it is oriented towards the uterotubal junction (Rasweiler, 1977*a*; Luckett, 1980). We confirmed this and noted a similar orientation in several other simplex phyllostomid bats, including *Phyllostomus, Anoura,* and *Ariteus.* Blastocyst orientation has not been recorded in any mormoopid and in our material (two specimens), orientation of the mass could not be determined. The evolutionary significance of implantation and blastocyst orientation is not entirely clear; future studies on mormoopids and *Macrotus*-group phyllostomids are needed to clarify the general nature of these phenomena in phyllostomoid bats.

Implications of Reproductive Histomorphology in Thyroptera

After the present study was completed, Wimsatt and Enders (1980) published a description of the uterus and placenta of *Thyroptera tricolor* (family Thyropteridae). They showed that *Thyroptera* shares derived uterine and placental features with noctilionids, mormoopids, and phyllostomids. From their account, it is clear that the uterus of *Thyroptera* is markedly fused externally, but has retained a relatively primitive internal uterine anatomy. Compared to phyllostomoid bats, external and internal uterine anatomy in *Thyroptera* is generally like noctilionids, although it appears that the thyropteran uterus may be somewhat more derived than that described for *Noctilio*. In any event, we concur with Wimsatt and Enders (1980) that *Thyroptera* shares the synapomorphy—external uterine fusion fused—with phyllostomoids.

The uterotubal junction of the thyropteran oviduct was noted by Wimsatt and Enders (1980) as being simple. In the present study, this feature was considered a synapomorphy of the superfamily Phyllostomoidea. Although Wimsatt and Enders (1980) did not detail oviductal histomorphology, one of their photomicrographs (233:fig. 4) shows the oviduct to possess mucosal folds in the intramural junctura, an arrangement similar to that found in noctilionids and mormoopids. These observations support the inclusion of thyropterids in a monophyletic group including noctilionids, mormoopids, and phyllostomids.

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TYPE SPECIMENS OF MAMMALS IN THE COLLECTION OF THE INSTITUTE OF BIOLOGY, NATIONAL UNIVERSITY OF MEXICO

Guillermina Urbano Vidales and Oscar Sanchez-Herrera

The mammal collection of the Institute of Biology was founded in 1945 by Dr. Bernardo Villa-Ramírez and has been growing steadily since that time, especially through the cooperation of a number of staff scientists. As of October 1982, the collection contained 19,939 specimens—17,394 skins accompanied by skulls, 2247 individuals in alcohol, and 298 complete skeletons.

These specimens represent 356 of the mammalian species occurring in México, based on published checklists such as those of Jones *et al.* (1977) and Hall (1981). All mammalian orders known to occur in México are present in the collection; Rodentia and Chiroptera are the orders best represented, which is not surprising, for rodents and bats together account for almost 75 per cent of the terrestrial species of mammals known from the country.

The collection also houses several type specimens, some of which (the bats) were reported on previously by Alvarez (1966). The present paper is intended to provide a complete and updated list of type materials in the Institute of Biology. Twenty-six type specimens exist, which relate to 15 taxa, as described below.

INSECTIVORA

Notiosorex (Xenosorex) phillipsii Schaldach

1966. Säugertierkund. Mitteil., 14:289, October.

Holotype.—Adult female, skin and skull, IBUNAM 8445, from Río Molino, 3 km SW San Miguel Suchixtepec, 2250 m, Oaxaca; obtained on 18 December 1964 by W. J. Schaldach, original number 13278.

Remarks.—Skin of right hind foot slightly damaged. A synonym of *Cryptotis mexicana peregrina* (Merriam, 1895) according to Choate (1970), even though the upper toothrow of the holotype (with three unicuspid teeth) does not seem to have any space corresponding to the supposedly missing fourth tooth.

CHIROPTERA

Balantiopteryx ochoterenai Martínez and Villa-R.

1938. An. Inst. Biol., Univ. Nac. Autón. México, 9:339, 14 November.

Lectotype.—Young adult male, specimen in alcohol with skull removed and tied to hind foot, IBUNAM 9180, from Cuautla, Morelos; obtained on 8 July 1938 by M. del Toro and Lic. Moreno, original number 30.

Remarks.—Skull lacking right zygomatic arch as well as part of the occiput; left wing membrane partly broken. This name is a synonym of *Balantiopteryx plicata plicata* Peters, 1867, as noted by Alvarez (1966), who designated no. 9180 as the lectotype.

Paralectotypes.—Adult female, IBUNAM 9179, original number 29; young female, IBUNAM 9181, original number 31; young female, IBUNAM 9182, original number 32; young female, IBUNAM 9183, original number 33; young female, IBUNAM 9184, original number 34. All paralectotypes are stored in alcohol and are from Cuautla, Morelos; obtained on 8 July 1938 by M. del Toro and Lic. Moreno.

Glossophaga morenoi Martínez and Villa-R.

1938. An. Inst. Biol., Univ. Nac. Autón. México, 9:347, 14 November.

"Neotype."—Adult female, skin and skull, IBUNAM 7383, from Cueva del Idolo, 1 km S Tequesquitengo, 950 m, Morelos; obtained on 24 April 1963 by M. Villa C. (W. A. Wimsatt), original number 37.

Remarks.—Right auditory bulla missing, left wing membranes perforated. Webster and Jones (1980) have placed this name as a synonym of *Glossophaga leachii*, an action with which we agree. In that context, we do not give nomenclatorial validity to this "neotype," because its dental features (such as procumbent upper incisors, evenly spaced lower incisors, depressed presphenoid ridge, and reduced pterygoid "wings") place it in *G. soricina.* Furthermore, the designation of neotype does not conform to the requirements of the International Code of Zoological Nomenclature, Article 75 (sections a and c). In any event, the specimen will be kept labeled as "neotype" for ease of reference.

Leptonycteris nivalis yerbabuenae Martínez and Villa-R.

1940. An. Inst. Biol., Univ. Nac. Autón. México, 11:313, August.

Paratypes.—Adult male, IBUNAM 9214, original number 269; adult female, IBUNAM 9215, original number 288; adult female, IBUNAM 9216, original number 294; from Cueva de la Laguna Honda, Yerbabuena, 1800 m, Guerrero; obtained on 15 September 1938 by L. Martínez; original numbers, if any, unknown. All specimens, from which the skulls have been removed, are stored in alcohol.

Remarks.—Hall (1981) gave full recognition to *L. yerbabuenae* as a valid species and provided a discussion on its nomenclatorial status (but see Watkins *et al.*, 1972). The three paratypes in our collection represent a species distinct from *L. nivalis* according to the systematic characters outlined by Hoffmeister (1957) and Hall (1981).

Ramírez and Alvarez (1972) designated no. 9216 as a "lectotype" and the other two specimens as "paralectotypes." However, as pointed out by Watkins *et al.* (1972), Article 72a of the International Code of Zoological Nomenclature indicates that a lectotype can be designated only from a syntypic series.

Vesperugo veraecrucis Ward

1981. Amer. Nat., 25:745, August.

Holotype.—Adult male, specimen in alcohol, IBUNAM 9243, from Las Vigas, Canton of Jalapa, Veracruz; obtained by H. L. Ward and C. M. Teran; date not recorded on the new label, which furthermore reads "cerca de Jalapa"; original number 527, recorded on a small rigid (probably wooden) label tied to the right foot.

Remarks.—The type has a hole (4 mm in diameter) in the abdominal region. This taxon currently is regarded as valid under the name *Pipistrellus subflavus veraecrucis.*

Paratypes.—Adult female, IBUNAM 9244, original number 528, and adult male, IBUNAM 9245, original number 531; both in alcohol; from the type locality; dates not recorded on labels, obtained by H. L. Ward.

Rhogeessa mira LaVal

1973. Occas. Papers Mus. Nat. Hist., Univ. Kansas, 19:26, 9 November.

Holotype.—Adult male, skin and skull, IBUNAM 8594, from 20 km N El Infiernillo, Michoacán; obtained on 29 November 1964 by Ticul Alvarez, original number 1896.

Remarks.—The holotype has the right half of uropatagium perforated. *R. mira* is a valid and monotypic species (Jones *et al.*, 1977; Hall, 1981).

Nyctinomus depressus Ward

1891. Amer. Nat., 25:747, August.

Holotype.—Adult male, specimen in alcohol with skull removed, IBUNAM 9246, from Tacubaya, Distrito Federal; date not recorded on label; presumably obtained by H. L. Ward, original number 516.

Remarks.—Skull lacking the right occipital condyle. Now a synonym of *Tadarida macrotis* (Gray, 1839)—see Hall (1981).

Cynomops malagai Villa-R.

1955. Acta. Zool. Mexicana, 1 (4):2, 15 September.

Holotype.—Adult female, skin and skull, IBUNAM 1738, from Tuxpan de Rodríguez Cano, 4 m, Veracruz; obtained on 2 August 1955 by B. Villa-R., original number 3847.

Remarks.—Actually a synonym of *Molossus ater nigricans* Miller, 1902—see Hall (1981).

RODENTIA

Citellus adocetus arceliae Villa-R.

1942. An. Inst. Biol., Univ. Nac. Autón. México, 13:357, October.

Paratype.—Adult male, skin and skull, IBUNAM 4436, from Rancho El Limón, 4 km S Arcelia, Guerrero; obtained on 11 December 1941 by B. Villa-R., original number 141.

Remarks.—Skin bald in several areas excepting the dorsal region and head. Now regarded as a synonym of *Spermophilus adocetus adocetus* Merriam, 1903—see Hall (1981).

Orthogeomys grandis alvarezi Schaldach

1966. Säugertierkund. Mitteil., 14:292, October.

Holotype.—Adult female, skin and skull, IBUNAM 8496, from 40 km N San Gabriel Mixtepec, Oaxaca; obtained on 13 December 1964 by W. J. Schaldach, original number 13271.

Remarks.—A valid subspecies following Hall (1981).

Orthogeomys grandis huixtlae Villa-R.

1944. An. Inst. Biol., Univ. Nac. Autón. México, 15:319.

Holotype.—Adult male, skin and skull, IBUNAM 221, from Finca Lubeca, 12 km N Huixtla, 850 m, Chiapas; obtained on 4 January 1944 by B. Villa-R., original number 362.

Remarks.—A valid taxon according to Hall (1981).

Tylomis gymnurus Villa-R.

1941. An. Inst. Biol., Univ. Nac. Autón. México, 12:763, 18 November.

Holotype.—Adult female, skin and skull, IBUNAM 101, from Presidio, Veracruz; obtained on 26 August 1940 by Abraham Ramírez, original number 2/161 (skin label).

Remarks.—Specimen in good condition except for slight damage to ears. The name *Tylomis* is a lapsus calami for *Tylomys.*

Paratype.—Adult male, skin and skull, IBUNAM 100, from Presidio, Veracruz; obtained on 26 August 1940 by Abraham Ramírez, original number 1/160 (skin label).

Remarks.—Skull has a broken interparietal, right parietal, and left supraoccipital. Villa-R. designated specimen 1/160, female, as the holotype; however, the original label of the male reads 1/160 and it is attached to the paratype. In addition, the date listed by Villa-R. in his work is 27 August 1940, and not the original date. This would suggest a mistaken sex-number correspondence in the original description. This is a valid subspecies, *Tylomys nudicaudus gymnurus,* according to Hall (1981).

Tylomys nudicaudus villai Schaldach

1966. Säugertierkund. Mitteil., 14:294, October

Holotype.—Adult female, skin and skull, IBUNAM 8516, from Km 183 (=36.5 km N by road) San Gabriel Mixtepec, 1600 m, Oaxaca; obtained on 13 December 1964 by Juan Nava Solorio, original number (W. J. Schaldach) 13276.

Remarks.—Hall (1981) regarded *T. n. villai* as a valid taxon.

CARNIVORA

Potos flavus dugesii Villa-R.

1944. An. Inst. Biol., Univ. Nac. Autón. México, 15:323, October.

Holotype.—Adult female, skin and skull, IBUNAM 212, from SE La Esperanza coffee plantation, 45 km NW Huixtla, 760 m, Chiapas; obtained on 2 January 1944 by B. Villa-R., original number 356.

Remarks.—Left side of nape bald and the left pml broken. Now regarded as a synonym of *Potos flavus chiriquensis* J. A. Allen 1904—see Kortlucke (1973) and Hall (1981).

Spilogale pygmaea intermedia López-Forment and Urbano

1979. An. Inst. Biol., Univ. Autón. México, 50(1):726.

Holotype.—Adult male, skin and skeleton, IBUNAM 12145, from 8 km E Chamela, 60 m, Jalisco; obtained on 27 May 1970 by W. López-Forment C., original number 354.

Remarks.—Hind feet slightly damaged; braincase broken and lacking the right temporal and parietal regions; occipital area separated, left zygomatic arch broken; left mandibular ramus broken, lacking coronoid and angular processes as well as condyle; rib cage almost complete (tenth and following ribs missing).

Paratypes.—Adult male, skin and partial skeleton, IBUNAM 14541 from 6 km E Chamela, 50 m, Jalisco; obtained on 4 October 1972 by C. Sanchez H. original number 1434. Adult male, skin and skull, IBUNAM 14542, from 6 km E Chamela, 60 m, Jalisco; obtained on 20 December 1973 by C. Sanchez H., original number 1797.

Remarks.—IBUNAM 14541 has the right maxilla and jugal separated from the skull, and the right I1, I2, and I3 missing, as are the premaxillae; other bones present are part of the vertebral column, and some ribs and limb bones.

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REDESCRIPTION OF CENTRUROIDES TESTACEUS (DEGEER) AND DESCRIPTION OF A NEW SPECIES FROM THE LESSER ANTILLES (SCORPIONES: BUTHIDAE)

W. David Sissom and Oscar F. Francke

Scorpio testaceus DeGeer was described in 1778 from specimens collected in "Amérique," and since that time references to that species have appeared many times in the literature. Thorell (1877) placed it in the genus *Centrurus* (= *Centruroides* Marx) but did not report a locality for the specimens he examined. Subsequent authors reported *C. testaceus* from Montserrat (Pocock, 1893), Hispaniola (Haiti) (Roewer, 1943), and southern Florida (Banks, 1900). The record for Florida has been discredited (Gertsch and Soleglad, 1966; Muma, 1967). Kraepelin (1895, 1899) considered *Tityus serenus* Koch (distribution unknown) and *Tityus griseus* Koch (from St. Thomas, U.S. Virgin Islands) to be synonyms of *C. testaceus*. Koch's specimen of *T. griseus* was recently examined, and Kraepelin's synonymy shown to be incorrect (Francke and Sissom, 1980).

Meise (1934) transferred all members of *Centruroides* to *Rhopalurus* Thorell and recognized four polytypic species, one of which was *R. testaceus*. A new subspecies, *R. testaceus exsul* Meise, was described from the Galápagos Islands. Hoffmann (1939) relegated all species to their former status, and *C. exsul* has subsequently been considered a valid species (Mello-Leitão, 1945; Kinzelbach, 1973). We have examined some speciments of *C. exsul* and agree with those authors; further, *C. exsul* does not appear to be closely related to *C. testaceus*, based on differences in carinal morphology

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of the pedipalps and metasoma, granulation of the mesosomal tergites, and morphometry.

We have been able to locate and examine the following material previously referred to as *Centruroides testaceus*: the two available syntypes of *Scorpio testaceus* DeGeer, Pocock's specimens from Montserrat, and Roewer's specimen from Haiti. In addition we have examined material from the nearby islands of Guadeloupe, St. Kitts, Nevis, Les Saintes, La Desiderade, and Marie Galante. Attempts to locate the type of *Tityus serenus* Koch have failed; Dr. W. R. Lourenço, who is currently studying that genus, informs us that the specimen is probably lost (personal communication). Likewise, we have been unable to locate Thorell's specimen(s).

Examination of the above specimens indicates that two distinct species are involved; in this paper their status is clarified. The material from the various islands is described as a new species, and the identity of the syntypes of *C. testaceus* is established. The specimen from Haiti studied by Roewer (1943), is a juvenile male (not a female as indicated by that author), most similar to the new species described below. However, in the genus *Centruroides*, juveniles of closely related species are very difficult to distinguish; thus, we are uncertain about the specific identity of the juvenile male from Haiti. Repositories for type material and specimens examined are referred to in the text by institutional acronyms, a key to which appears in the acknowledgments section.

Centruroides pococki, new species
(Figs. 1-9)

Centrurus testaceus: Thorell, 1877:160 (in part ?); Kraepelin, 1891:130 (misidentification), 1895:95 (misidentification), 1899:91 (misidentification); Pocock, 1893:389, pl. 30, figs. 11, 11a (misidentification); Waterman, 1950:168 (misidentification).

Rhopalurus testaceus: Meise, 1934:30-36 (misidentification).

Centruroides testaceus: Werner, 1934:274 (misidentification); Francke, 1978:70 (misidentification); Schawaller, 1979:14 (misidentification); Francke and Sissom, 1980:1 (misidentification).

Centruroides testaceous: Stahnke and Calos, 1977:112, 117, 119 (misidentification); Stahnke, 1978:280 (misidentification).

Centruroides sp.: Armas, 1982:7

Type data.—Adult male holotype, cat. no. RS-6234, from Guadeloupe, "dans un ilôt, côte sous le vent sous les galets des plages," 1-II-1963 (J. L. Raton); deposited MNHN, Paris.

Distribution.—Known from the Lesser Antillean islands of St. Kitts, Nevis, Montserrat, Guadeloupe, Les Saintes, La Desiderade, and Marie Galante.

Etymology.—The specific name is a patronym honoring Mr. R. I. Pocock for his contributions to scorpion systematics.

Diagnosis.—Adults 65-75 mm in length. Golden brown with variable underlying fuscosity; pedipalp fingers and distal segments of metasoma brownish. Tergites I-VI monocarinate, VII pentacarinate, all carinae strong. Sternite VII weakly tetracarinate. Pectinal tooth count in males 20-23 (mode 22), in females 19-22 (mode 20). Metasomal carinae moderate on I-IV in both sexes. Telson with subaculear tubercle weak to obsolete. Pedipalp chela fixed finger with eight rows of denticles (Fig. 3), movable finger with eight rows of denticles and a short apical row of four denticles (Fig. 4); inner and outer supernumerary granules present on both fingers. Ratio of metasoma V length to carapace length averaging 1.43 (range = 1.36-1.48, *N* = 9) in males, 1.10 (range = 1.06-1.13, *N* = 12) in females. Ratio of fixed finger length to carapace length averaging 0.99 (range = 0.93-1.06, *N* = 22).

Description.—The following description is based on males; parenthetical statements refer to females. Measurements of the holotype male and a paratype female appear in Table 1.

Prosoma. Carapace: anterior margin emarginate. Anterior median furrow moderately wide, deep; posterior median furrow wide, deep; posterior lateral furrows wide, deep, curved; other furrows inconspicuous. Superciliary, lateral ocular, central ocular, and posterior median carinae moderate, coarsely granular; other carinae less distinct. Interocular region densely and coarsely granular; remainder of carapace with less dense, coarse granulation. Sternum: subtriangular, with deep anteriorly directed Y-shaped longitudinal furrow.

Mesosoma. Pretergites shagreened; post-tergites coarsely granular. Median longitudinal carina on tergites I-II (I-III) moderate, coarsely granular; on III-VI (IV-VI) strong, coarsely granular. Tergite VII pentacarinate: median carina strong, granular; submedian and lateral carinae strong, coarsely granular. Venter: genital operculum completely divided longitudinally, genital papillae small (absent). Pectinal basal piece with median depression (large median depression and two small elliptical lateral depressions); pectinal tooth count 20-23, mode 22 (19-22, mode 20). Sternites III-VI smooth; sternite VII tetracarinate, submedian and lateral carinae moderate (weak), finely serrate.

Metasoma. Segments I-IV: All carinae moderate. Dorsolateral carinae on I finely serrate, converging posteriorly; on II-III finely serrate (serratocrenulate); on IV crenulate. Lateral supramedian carinae on I finely serrate (serratocrenulate); on II finely serrate to crenulate (serratocrenulate); on III-IV weakly crenulate (serrato-

TABLE 1.—*Measurements (in mm) of* Centruroides testaceus *(DeGeer) and* Centruroides pococki, *new species.*

	C. testaceus	*C. pococki*	
	lectotype	holotype ♂	paratype ♀
Total length	66.5	71.0	67.7
Carapace length	6.3	6.2	7.2
Mesosoma length	16.5	18.8	20.2
Metasoma length	36.8	38.9	32.7
I length/width	5.5/3.4	6.0/2.6	5.1/3.3
II length/width	6.8/3.3	7.3/2.5	6.1/3.2
III length/width	7.4/3.1	7.8/2.4	6.4/3.2
IV length/width	8.3/2.9	8.5/2.4	7.1/3.1
V length/width	8.8/2.8	9.3/2.5	8.0/3.1
Telson length	6.9	7.1	7.6
Vesicle length	4.1	5.2	4.8
width	2.3	2.5	2.7
depth	2.2	2.2	2.4
Aculeus length	2.8	2.3	3.2
Pedipalp length	25.4	25.3	27.1
Femur length	6.2	6.6	7.0
width	1.6	1.5	1.8
Tibia length	7.2	7.2	7.6
width	2.3	2.1	2.5
Chela length	12.0	11.5	12.5
width	2.6	2.6	2.8
depth	2.9	2.6	2.9
Movable finger length	7.3	7.1	8.2
Fixed finger length	6.6	6.2	7.2
Pectinal teeth (left-right)	28-28	22-23	21-21

crenulate). Lateral inframedian carinae on I complete, finely serrate; on II-IV absent. Ventrolateral carinae on I finely serrate (serratocrenulate); on II-IV weakly crenulate (crenulate). Ventral submedian carinae on I finely serrate; on II finely serratocrenulate; on III-IV crenulate. Intercarinal spaces of segments I-IV with coarse granulation. Segment V (Figs. 6, 8): Dorsolateral and lateral median carinae obsolete; on some specimens very weak, granular. Ventrolateral carinae weak, granular. Ventromedian carina moderate, weakly crenulate (crenulate). Intercarinal spaces with dense coarse granulation.

Telson (Figs. 7, 9). Vesicle less than twice as long as wide; moderately slender (moderately globose); ventral surface granular (densely granular); subaculear tubercle weak, vestigial, or obsolete. Aculeus length approximately 0.50 (0.65) that of vesicle length, moderately (sharply) curved.

Chelicera. Dentition typical of genus; basalmost tooth of movable cheliceral finger sometimes reduced.

Pedipalp. Femur: tetracarinate, with all carinae moderate. Dorsointernal carina serratocrenulate (crenulate); dorsoexternal carina serratocrenulate (serratocrenulate to serrate); ventrointernal carina crenulate (serratocrenulate); ventroexternal carina serrate (serratocrenulate). Internal face with row of large conical granules. Orthobothriotaxia "A" (Vachon, 1974).

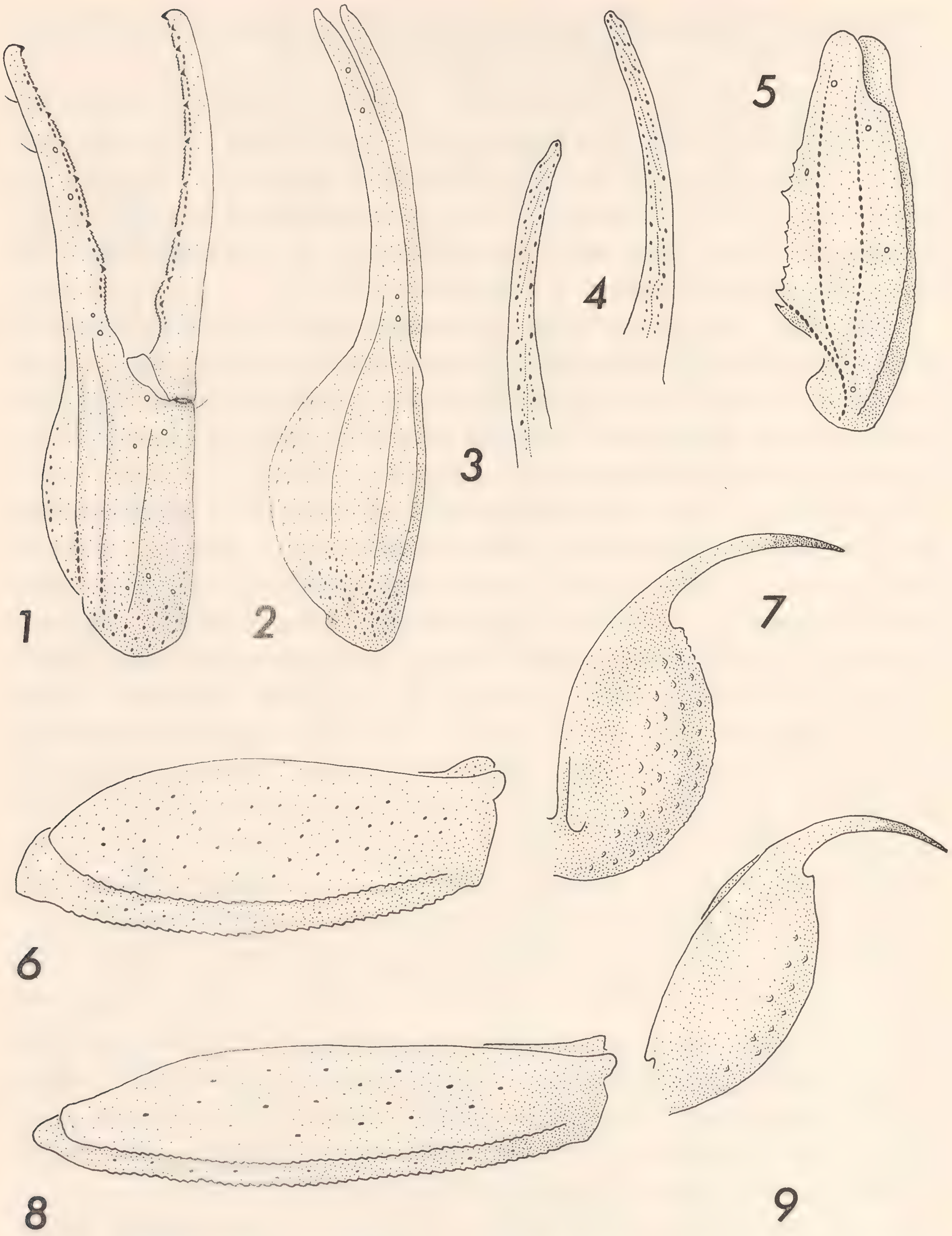
Tibia (Fig. 5): hexacarinate, all carinae moderate. Dorsointernal carina crenulate; dorsomedian, dorsoexternal, and external carinae weakly crenulate; ventrointernal carina granular; ventroexternal carina weakly crenulate. Internal face with row of large conical granules. Orthobothriotaxia "A" (Vachon, 1974).

Chela (Figs. 1-4): Fixed finger (Fig. 3) with eight oblique rows of granules; movable finger (Fig. 4) with eight oblique rows of granules plus a short apical row of four granules; supernumerary granules present in later instars, absent in early instars. Fingers moderately scalloped basally. Dorsal marginal carina moderate (weak), granular basally, smooth to granular distally. Dorsal secondary carina moderate (weak), granular basally, smooth to granular distally. Digital carina moderate, granular basally, smooth to granular distally. External secondary carina weak, granular. Ventroexternal carina moderate, smooth to granular. Ventrointernal carina weak, smooth. Internal surface with numerous small, sharp granules. Orthobothriotaxia "A" (Vachon, 1974).

Coloration. Carapace and tergites golden brown; lateral eyes and ocular tubercle black; chelicerae creamy white. Metasoma golden brown, in many specimens gradually becoming orange brown distally; telson golden brown to orange brown. Pedipalps: femur, tibia, and chela manus golden brown; chela fingers dark brown. Legs yellow. Carapace, chelicerae, tergites, metasoma, pedipalps, and legs with variable underlying fuscosity.

Variation.—The following characters were found to be markedly variable among adults in *C. pococki*: (1) coloration, (2) pectinal tooth counts, and (3) the size of the subaculear tubercle. Coloration differs primarily in the amount of underlying fuscosity. There is a gradation from an almost immaculate condition to one of rather dense fuscosity.

Pectinal tooth counts in males were found to vary as follows: 3 combs with 20 teeth (15%); 2 combs with 21 teeth (10%); 8 combs with 22 teeth (40%); and 7 combs with 23 teeth (35%). Pectinal tooth counts in females were found to vary as follows: 1 comb



Figs. 1-9.—External anatomy of *Centruroides pococki*, new species: 1, external aspect of right pedipalp chela; 2, dorsal aspect of right pedipalp chela; 3, dentate margin of fixed finger; 4, dentate margin of movable finger; 5, dorsal aspect of right pedipalp tibia; 6, lateral aspect of metasomal segment V of female; 7, lateral aspect of telson of female; 8, lateral aspect of metasomal segment V of male; 9, lateral aspect of telson of male.

with 19 teeth (3.6%); 14 combs with 20 teeth (50%); 9 combs with 21 teeth (32.1%); and 4 combs with 22 teeth (14.3%).

The subaculear tubercle varies from obsolete to weak among specimens examined. In addition, the shape of the telson (Figs. 7,

9) and the lengths of the metasomal segments (Figs. 6, 8, Table 1) were found to be sexually dimorphic, as is typical of other *Centruroides*. Juveniles differ from adults by being very pale yellow with stronger underlying fuscosity and by lacking the characteristics of sexual dimorphism discussed above.

Comparisons.—*C. pococki* is most similar to *C. testaceus* (DeGeer), with which it has been confused in the past. From that species it differs markedly in pectinal tooth counts (in *C. pococki*, males range from 20-23 in this character and females from 19-22; the lectotype and only known specimen of *C. testaceus*, a female, has a count of 28-28). In *C. pococki* the ventrolateral and ventral submedian carinae of the metasoma are moderate, in *C. testaceus* they are weak. The shape of the telson also differs (see Figs. 7, 16), being more globose in *C. pococki*. Finally, the metasomal segments of *C. testaceus* are proportionately longer than those of *C. pococki*: the female of *C. testaceus* has a metasomal segment V length/carapace length ratio of 1.40; in females of *C. pococki* this ratio ranges from 1.06-1.13. *Centruroides pococki* may also be easily distinguished from *Centruroides hasethi* Pocock by its lower pectinal tooth counts.

Specimens examined.—LESSER ANTILLES: *Saint Kitts*: Old Bay Road, April 1969 (F. D. Bennett, 4 ♂♂, 3 ♀♀, 7 juv. (ENKW-604) (FSCA); Brimstone Hill, 13 April 1967 (F. D. Bennett and R. Yearwood), 1 ♀ (ENKW-462) (FSCA), 21 June 1967 (F. D. Bennett, K. Lawrie, and J. Phillips), 1 ♂, 4 ♀♀ (ENKW-490) (FSCA); *Nevis*: Indian Castle, 20 November 1967 (F. D. Bennett), 1 ♀, 1 juv. (ENKW-601) (FSCA); *Montserrat*: no date (no collector), 3 ♂♂, 2 ♀♀ (BMNH); *Guadeloupe*: Anse-a-l'eau (bajo piedras), 3 March 1975 (F. Chalumeau), 1 ♂, 2 ♀♀ (ACC/IZ), 18-I-1977 (F. Chalumeau), 1 ♀ (RS-8121), 1 juv. (RS-8118) (MNHN); "Dans un ilôt, côte sous le vent sous les galets des plages", 1-II-1963 (J. L. Raton), 1 holotype ♂, 1 ♂, 2 ♀♀ (RS-6234) (MNHN); Grandes Salines, Pointe des Chateaux (sous pierres.), 10-XII-1978 (J. d'Aguilar), 1 ♂, 1 ♀ (RS-7334) (MNHN); Grande Terre, La Grande Vigie (sus le picore en sus bois), 17-IV-1979 (J.-P. Mauries), 1 ♀, 1 juv. (RS-7376) (MNHN); Pte, de la Grande Vigie ("causse" tres sec a "Crabes"), 3 Juin 1978 (J.-P. Mauries), 1 ♀, 1 juv. (RS-7284) (MNHN); St. François, Pte. des Chateaux [pres croix (sous pierre.) très sec.], 6 Juin 1978 (J.-P. Mauries), 1 ♀ (RS-7282) (MNHN); *Les Saintes*: Terre de Haut, Le Chameau (309 m), 17 Juin 1978 (J.-P. Mauries), 1 ♂, 1 ♀, 1 juv. (RS-7283) (MNHN), Terre de Haut, 6-III-1976 (F. Chalumeau), 1 ♂ (RS-8119) (MNHN); *Marie Galante*: Capestere les Galets, 5-II-1978 (Chalumeau), 3 ♀♀ (RS-8336) (MNHN).

Centruroides testaceus (DeGeer)

(Figs. 10-17)

Scorpio testaceus DeGeer, 1778:347, pl. 41, fig. 11.

Centrurus testaceus: Thorell, 1877:160 (in part); *nec* Kraepelin, 1891:130, 1895:95, 1899:91; *nec* Pocock, 1893:389; *nec* Banks, 1900:425; *nec* Waterman, 1950:168; Gertsch and Soleglad, 1966:1.

Centruro testaceo: Karsch, 1879:120.
Rhopalurus testaceus: *nec* Meise, 1934:30-36.
Centruroides testaceus: *nec* Werner, 1934:274; Hoffmann, 1939:322, 324; *nec* Roewer, 1943:219; Bücherl, 1971:327; *nec* Francke, 1978:70; *nec* Schawaller, 1979:14; *nec* Francke and Sissom, 1980:1; Armas, 1982:7.
Centruroides testaceous (*sic*): *nec* Muma, 1967:16; *nec* Stahnke and Calos, 1977:112, 117, 119; *nec* Stahnke, 1978:280.

Type data.—DeGeer (1778) described *Scorpio testaceus* from at least two specimens. We have examined the two available syntypes (a female and a male) and they are not conspecific. Whereas the original description applies to both specimens, the female is illustrated (1778:pl. 41, fig. 11) and is presently in better condition than the male. For these reasons, the female is hereby designated lectotype. Both specimens are dried and pinned. The lectotype female and the unidentified male are deposited in NHR, Stockholm.

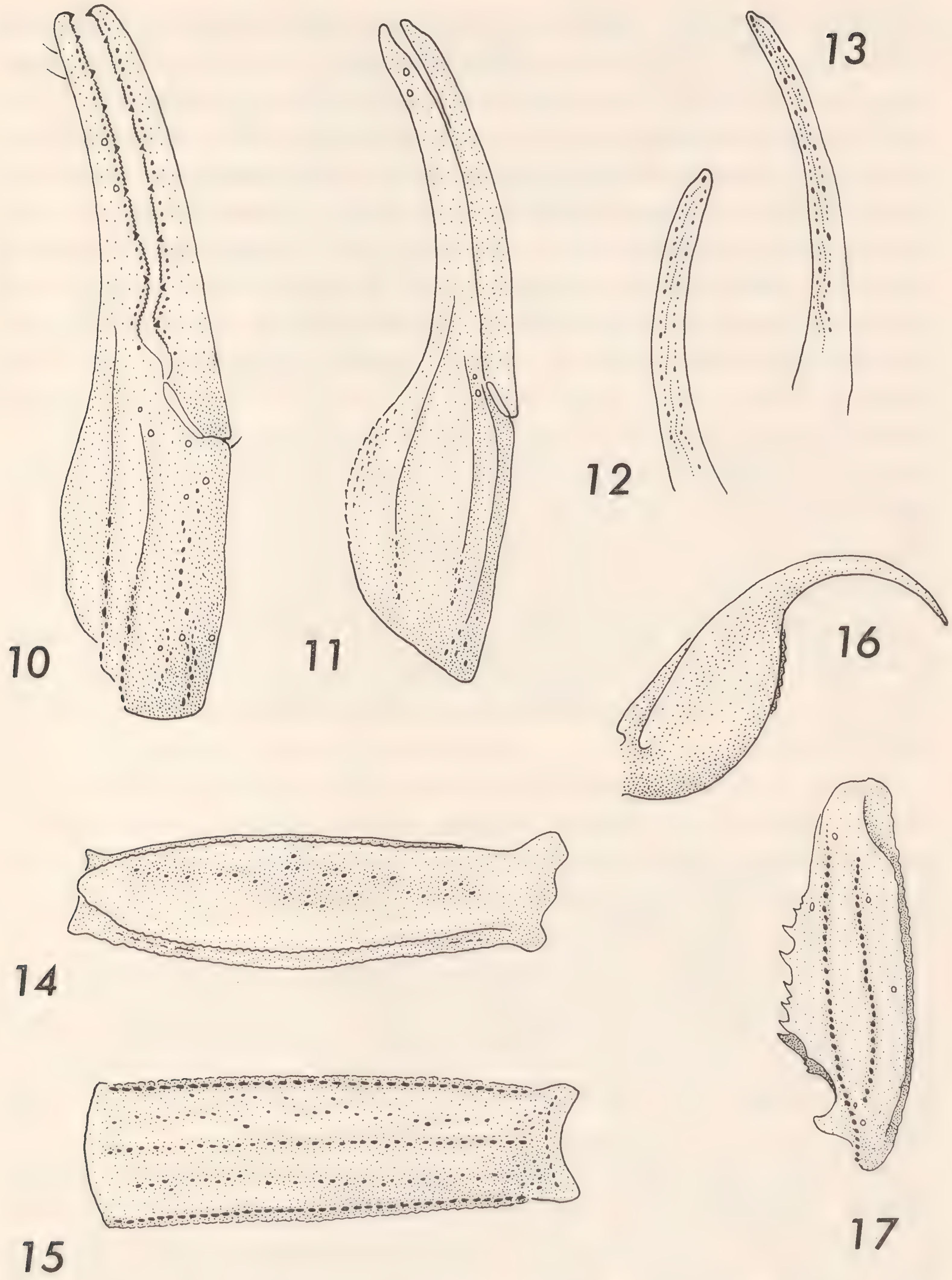
Distribution.—Known only from "Amérique".

Diagnosis.—Based on adult female lectotype. Total length 66.5 mm. Present coloration golden brown, immaculate. Tergites I-VI monocarinate, VII pentacarinate, all carinae strong. Sternites III-VI acarinate, VII weakly tetracarinate. Pectinal tooth count 28. Ventrolateral and ventral submedian carinae of metasoma weak, others moderate. Telson (Fig. 16) with ventral row of small granules, lacking definite subaculear tubercle. Pedipalp chela fixed finger with eight rows of denticles, movable finger with eight rows of denticles and short apical row of four denticles; inner and outer supernumerary granules present on both fingers. Ratio of metasoma V length to carapace length 1.40; of fixed finger length to carapace length 1.05.

Description.—The following description is based on the female lectotype. Measurements appear in Table 1.

Prosoma. Carapace: anterior margin moderately notched. Anterior median furrow moderately wide, deep; posterior median furrow wide, deep; posterior lateral furrows wide, deep, curved; other furrows inconspicuous. Superciliary, lateral ocular, and posterior median carinae moderate, coarsely granular; central lateral carinae moderately strong, coarsely granular; other carinae poorly defined. Interocular region densely and coarsely granular; remainder of carapace with scattered, coarse granulation. Sternum: subtriangular, with deep anteriorly directed Y-shaped longitudinal furrow.

Mesosoma. Pretergites shagreened; post-tergites coarsely granular. Median longitudinal keel on tergites I-III weak, coarsely



FIGS. 10-17.—External anatomy of *Centruroides testaceus* (DeGeer): 10, external aspect of right pedipalp chela; 11, dorsal aspect of right pedipalp chela; 12, dentate margin of fixed finger; 13, dentate margin of movable finger; 14, lateral aspect of metasomal segment V; 15, ventral aspect of metasomal segment V; 16, lateral aspect of telson; 17, dorsal aspect of right pedipalp tibia.

granular; on IV-VI moderate, coarsely granular. Tergite VII pentacarinate: median keel moderate, granular; submedian keels moderate, crenulate; lateral keels moderate, crenulate. Venter: Genital operculum of lectotype damaged. Pectines with basal piece twice as broad as long, with two small lateral depressions; pectinal tooth count 28-28. Sternites III-VI smooth; sternite VII tetracarinate, submedian and lateral carinae weak, finely granular.

Metasoma. Segments I-IV: dorsolateral carinae on I moderate, finely crenulate, converging posteriorly; on II moderate, crenulate; on III-IV weak, finely crenulate to granular. Lateral supramedian carinae on I moderate, finely crenulate; on II moderate, crenulate; on III-IV weak, finely crenulate. Lateral inframedian carinae on I moderate, complete, granular to finely crenulate; on II-IV absent. Ventrolateral carinae on I weak, smooth on anterior one-half, finely granular on posterior one-half; on II-IV weak, finely crenulate. Ventral submedian carinae on I weak, smooth; on II weak, smooth on anterior one-half, finely crenulate on posterior one-half; on III-IV weak, finely crenulate. Dorsal face of segment IV with strong median longitudinal furrow; other intercarinal spaces of segments I-IV shagreened. Segment V (Figs. 14, 15): Dorsolateral, lateromedian, and ventrolateral carinae weak, granular; ventromedian carina moderate, granular. Ventral and lateral faces with fine granulation, dorsal face with moderate median longitudinal furrow.

Telson (Fig. 16). Vesicle less than twice as long as wide; moderately compressed dorsoventrally; ventral surface with row of small granules medially; no definite subaculear tubercle. Aculeus long, about two-thirds length of vesicle, sharply curved.

Chelicera. Dentition typical of genus.

Pedipalp. Femur: tetracarinate. Dorsointernal and dorsoexternal carinae moderate, granular to crenulate; ventrointernal and ventroexternal carinae moderate, serrate. Internal face set with a row of large conical granules. Orthobothriotaxia "A" (Vachon, 1974).

Tibia (Fig. 17): hexacarinate. Dorsointernal and dorsal median carinae moderate, granular. Dorsoexternal, external, ventrointernal, and ventroexternal carinae weak, granular. Internal face set with a row of large conical granules. Orthobothriotaxia "A" (Vachon, 1974).

Chela (Figs. 10-13): fixed finger (Fig. 12) with eight oblique rows of granules; movable finger (Fig. 13) with eight oblique rows of granules plus a short apical row of four granules; supernumerary granules present. Fingers moderately scalloped. Dorsal marginal carina weak to moderate; granular basally, smooth distally. Dorsal secondary and digital carinae moderate, granular basally, smooth distally. External secondary carina weak, granular. Ventroexternal carina moderate, smooth. Ventrointernal carina weak, granular. Internal surface of hand with numerous small, sharp granules. Orthobothriotaxia "A" (Vachon, 1974).

Coloration. The lectotype is a dry, pinned specimen and, therefore, its present coloration is unreliable. However, it appears that the specimen was uniformly colored, lacking the dark dorsal stripes characteristic of many species of the genus. There is also no suggestion of dusky markings on the legs, pedipalps, or body, or of darkening of the pedipalp chelae fingers; however, such markings are probably more subject to fading than dark dorsal stripes.

Comparisons.—Centruroides testaceus is similar to *C. hasethi* Pocock and *C. pococki* Sissom and Francke. It differs from *C. hasethi* by having a thinner and longer metasoma. The ratio of caudal segment V length/width is less than 2.40 in females of *C. hasethi*, 3.14 in *C. testaceus*; the ratio of caudal segment IV length/width is greater than 2.25 in females of *C. hasethi*, 2.86 in *C. testaceus*. Comparisons of *C. testaceus* to *C. pococki* appear in the appropriate section under the latter's description.

Specimens examined.—The lectotype female.

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ASPECTS OF THE THERMAL BIOLOGY OF THE BOLSON TORTOISE, GOPHERUS FLAVOMARGINATUS

Francis L. Rose

There are four extant species of tortoises in North America (*Gopherus agassizii, G. berlandieri, G. flavomarginatus, G. polyphemus*). *G. polyphemus* inhabits mesic regions of the southeastern United States, but the other three species inhabit xeric regions of the southwestern United States and northern Mexico. Despite the fact that these tortoises are a conspicuous component of their environment, until recently little was known about their thermal biology. Woodbury and Hardy (1948), McGinnis and Voigt (1971), and Voigt (1975) reported thermal values for *G. agassizii*; Judd and Rose (1977) and Voigt and Johnson (1976) reported thermal values for *G. berlandieri*; and Douglass and Layne (1978) reported data accumulated during an 8-year study of *G. polyphemus*. The critical thermal maxima were determined for *G. agassizii* and *G. berlandieri* (Hutchison *et al*, 1966; Brattstrom, 1965; Judd and Rose, 1977). Lowe *et al*. (1971) reported freezing points and supercooling limits of *G. agassizii* and *G. berlandieri*, and Spray and May (1972) reported heating and cooling rates of four species of chelonian, including *G. polyphemus*. No data have been published on the thermal biology of *G. flavomarginatus*.

The bolson tortoise, *G. flavomarginatus*, is the largest terrestrial chelonian occurring naturally in North America. Because of its restrictive range in an inhospitable environment and its secretive behavior, few data have been published on its biology. The species inhabits a limited area of about 10,000 km^2 in northern Mexico (southwest Coahuila, southeast Chihuahua, and northeast

Durango), although its range probably extended into what is now New Mexico and Arizona during the Pleistocene (Auffenberg, 1966).

This large tortoise is similar to *G. polyphemus* and *G. agassizii* in that all three species may construct extensive burrows. These burrows provide protection from unfavorable climatic conditions and from predators and probably are important in reducing evaporative water loss. In addition, the burrow entrance serves as a focal point of courtship activity for *G. polyphemus* (Douglass and Layne, 1978) as well as a primary site of egg-laying.

Two male *G. flavomarginatus* were maintained by the author in an outside enclosure (8 by 18 m) for eight years. In view of the paucity of information concerning the biology of this species, records were maintained of their behavior and body temperatures during this period. Beginning in May 1977, a detailed study of their thermal characteristics was made and the accumulated data form the basis of this report.

Materials and Methods

The two male tortoises used in this study measured 30.0 cm and 32.0 cm total carapace length. They had free access to move inside the enclosure, fed primarily on grasses even though cactus (*Opuntia lindheimeri*) was available, and drank after rains or when the vegetation was watered. The enclosure was shared with numerous adult *G. berlandieri* and one adult female *G. polyphemus*.

The study was begun on 23 May when the tortoises emerged from their burrow and was continued until 16 October 1977 when they retreated for the winter. Temperatures were taken in Celsius, with a Yellow Springs telethermometer, and included the following: body temperature (TB), which was taken through the cloaca at an insertion depth of 8 cm; solar radiation temperature (TAsun), which was taken at a point 8 cm above the ground with the probe fully exposed; and shade temperature (TAshade), which was taken 8 cm above the ground at one of two places, depending on the circumstances. Both shaded areas were extensive and were accessible to the tortoises. Burrow temperature (TAburrow) was taken at a depth of 50 cm with the probe free of the substrate. Time (CDST) was noted when the temperatures were determined.

The tortoise's behavior at the time that the temperatures were taken was divided into five categories: basking, courting (with the female *G. polyphemus*), feeding, walking (but not feeding), and inactive (but not basking).

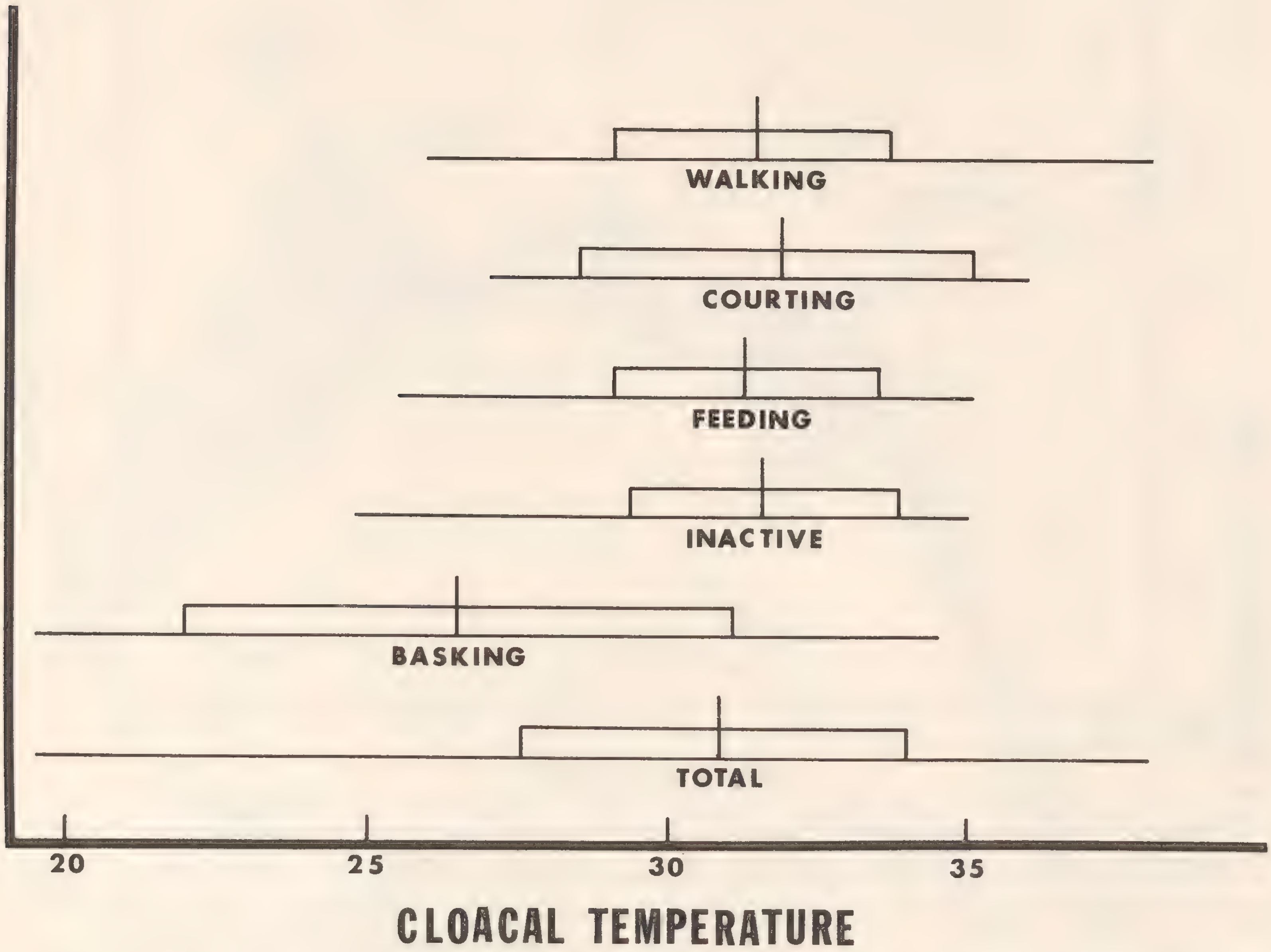

FIG. .1.—Mean, range, and standard deviation of cloacal temperatures (TBs) of *Gopherus flavomarginatus* separated as to behavior.

On 5 June, TB, TAsun, TAshade and TAburrow were recorded beginning at 0845 hrs and continuing approximately each hr until 2230 hrs. The tortoises did not use the burrow on this day but used a large patch of cactus as a thermal shield. TBs were taken regardless of the tortoise's behavior at the designated time.

Data were synthesized and analyzed using SAS through the Texas Tech University Computer Center. Results are expressed as the mean ± standard deviation (range). Differences in means were tested with a one-way ANOVA using an *F*-test. An analysis of covariance was employed to evaluate the slopes obtained when the TBs for before and after 1200 hrs were regressed against TAsun.

RESULTS

The overall mean TB for 181 observations was 30.8±3.2(19.5-38.0) (Fig. 1). If the TBs for basking were eliminated from the calculations, mean TB was 31.5±2.2(24.8-38.0). Only 20 per cent of the observations were below 30°, and the most frequent observations were 32 and 33° (41%). The TB of 38° was unique, and the most frequent observations were 32 and 33°, and no TBs of 36 or 37° were recorded. Only 12 per cent of the observations (excluding basking) were below 33°.

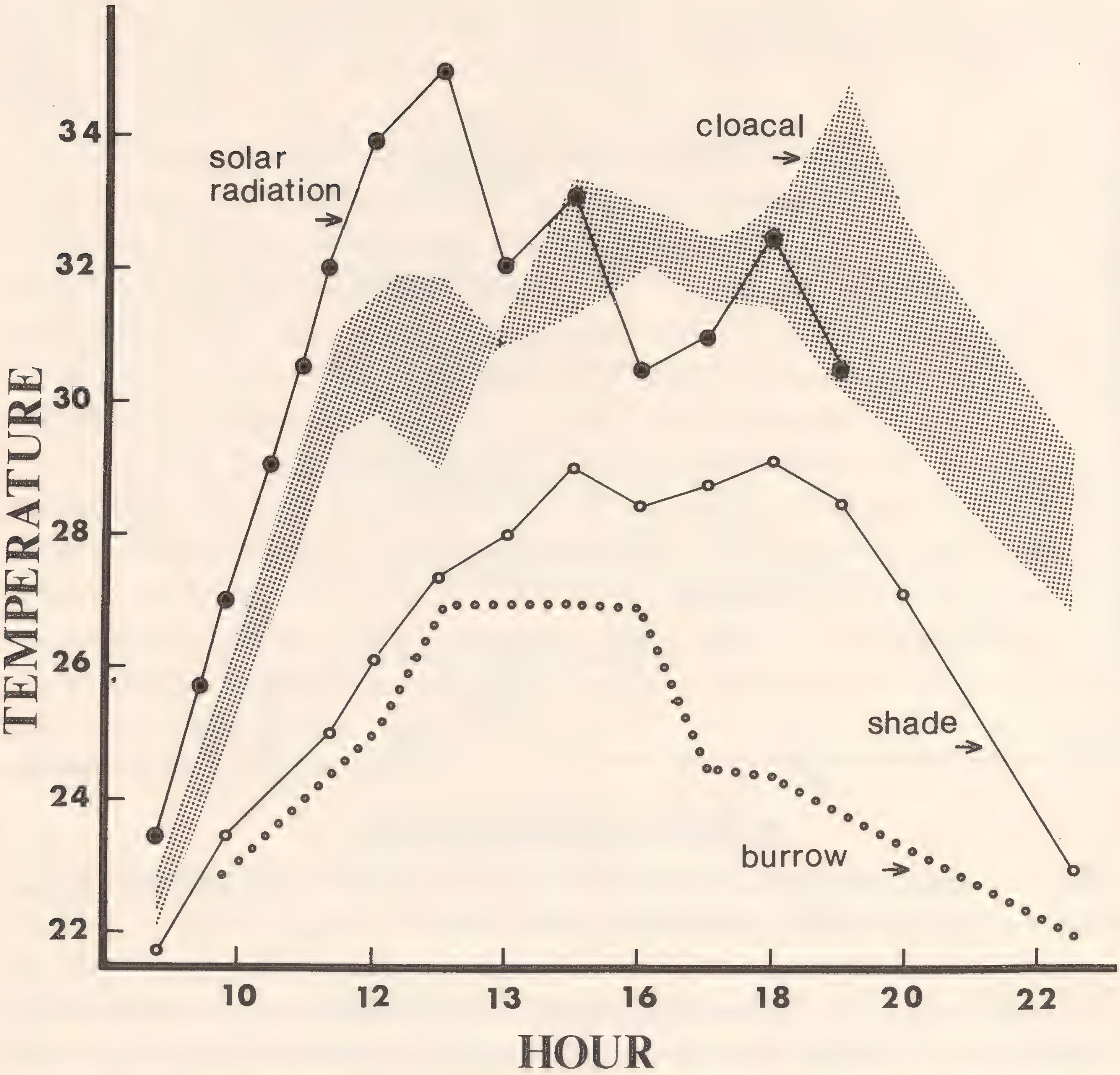

FIG. 2.—Changes in cloacal (TBs), solar radiation (TAsun), shade (TAshade), and burrow temperatures against time of day (CDST).

Generally a tortoise would bask until its TB reached 29-30°. Then it would move either to partial shade, to the burrow, or to the opposite end of the enclosure. When a tortoise remained overnight at the end of the enclosure away from the burrow it could not bask effectively in the morning due to shade and subsequently would move near the burrow to bask.

Mean TB during basking was 26.5±4.6(19.5-34.5). Because basking is a method of elevating TB, TB is a function of the intensity of solar radiation as well as the time spent basking. Thus, in the vast majority of cases the TB measured during basking would have increased had the tortoise's behavior not been altered. To avoid this obvious bias the basking temperatures were eliminated from the calculations unless noted.

Judd and Rose (1977) found no difference between morning and afternoon TBs of *G. berlandieri*. This was not the case for *G. fla-*

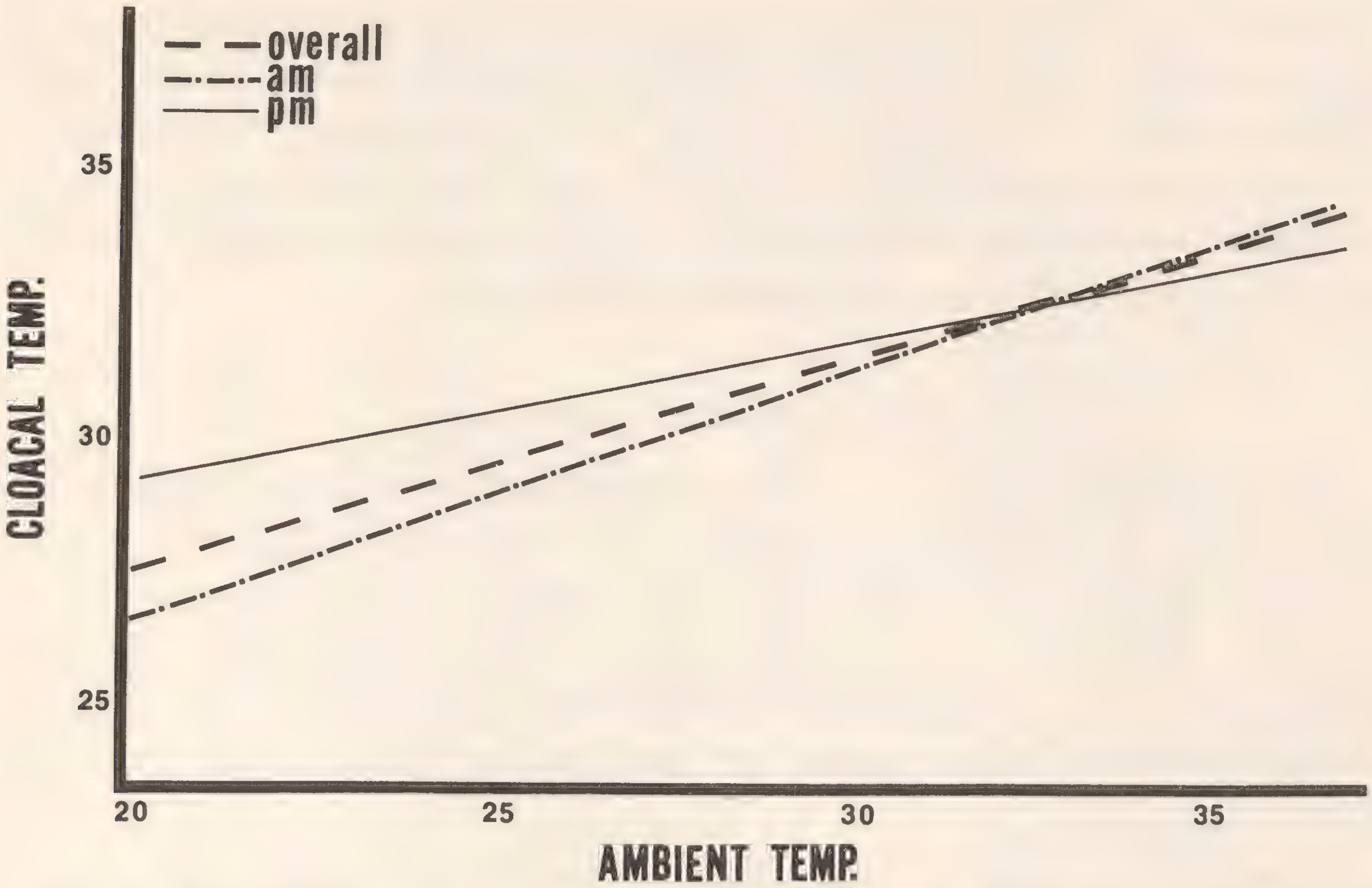

FIG. 3.—Regression lines of cloacal temperatures (TBs) against ambient temperature (TAsun). The three lines represent all of the data, and data collected prior to and after 1200 hrs. Analysis of covariance confirmed that two lines did not significantly enhance interpretation of the data.

vomarginatus for which the mean TB before 1200 hrs was 29.6±1.9 (24.8-32.5); the value after 1200 hrs was 32.2±1.89(25.0-38.0) (F^{1}_{153} = 59.4, $P<0.0001$).

Analysis of covariance confirmed that the overall TB data were positively correlated with TAsun before (F^{3}_{177} = 98.0, $P<0.0001$) and after (F^{3}_{151} = 86.9, $P<0.0001$) the basking temperatures were removed from the calculations (Fig. 2). In the absence of the basking temperatures, the test confirmed that two lines did not significantly (t=1.18, P±0.239) enhance a description of the relationships between TBs before and after 1200 hrs and TAsun.

The tortoises were occasionally observed basking in the afternoon. On 11 such occasions, the TB of a tortoise was ascertained while it fed and again within 30 minutes after feeding, while it basked. The mean TB was significantly higher after feeding: before, $\bar{\chi}$ = 30.3±1.28(28-32); after, $\bar{\chi}$ = 33.0±(32-34) (F^{1}_{20} = 32.2, $P<0.0001$).

Mean TBs of tortoises engaged in feeding, walking, courting, or inactivity were not different from overall values or from each other (Fig.1). No tortoise was observed feeding with a TB below 25.5° or courting with a TB less than 27°.

Fig. 3 depicts the relationships between TB, TAsun, TAshade, and TAburrow during a single day. Rate of change for TB and

TAsun was similar in the morning, but as TB neared 30° the tortoises altered their behavior and the hiatus between TAsun and TB increased. As TAsun decreased in the afternoon, the tortoises became more active, more exposed, and their TBs increased to exceed morning post-basking TBs. In fact, TB was highest in the afternoon when TAsun was stable or decreasing.

Comparisons and Discussion

The preferred TB of *G. flavomarginatus* does not appear to differ from that of the other species of *Gopherus* (Table 1). If differences were to be observed, one might expect them to have occurred between *G. polyphemus* and the other three species inasmuch as *G. polyphemus* is the only member of the genus which inhabits mesic areas; or, between *G. berlandieri* and its larger congeners.

Comparisons of the mean TBs of *Gopherus* species and other chelonians are tenuous because there are few terrestrial species of comparable size inhabiting the arid and semiarid regions of North America. *Terrapene ornata* is one of the few, and data have been accumulated on its TB (Fitch, 1956; Legler, 1960). It would appear that this terrestrial emydine has a slightly lower preferred temperature than members of the genus *Gopherus*; however, the important point may be that *T. ornata* is eurythermal in regards to its activity. On overcast days at TAs or TBs below 25°, *T. ornata* may feed actively; *Gopherus* species do not. The herbivorous habit of *Gopherus* may demand high temperatures to facilitate digestion and assimilation of food stuffs.

Burrow temperatures, even in the deserts of the southwest, may be below the optimum temperature needed for proper digestion and assimilation by the tortoises. The observed basking of *G. flavomarginatus* after feeding might represent a behavior to foster digestion. Such a limitation placed on proper digestion may well account for the inordinate amount of time the tortoises spend in and near the burrow entrance.

Hutchison *et al.* (1966) noted that of the 25 species of chelonia tested, the terrestrial testudinids had the highest critical maxima: *G. berlandieri* = 42.8°, *G. agassizii* = 43.1°; and, *G. polyphemus* = 43.9°. The CTM for *G. flavomarginatus* was not determined. However, the combined evidence indicates that the *Gopherus* species are physiologically adapted to comparatively high temperatures.

Differences in TBs of *G. flavomarginatus* prior to and after 1200 hrs are due to differences in TAsun, the large size of the tor-

TABLE 1.—*Summary of the thermal aspects of the four species of* Gopherus. *Modified after Judd and Rose (1977).*

MTB	Min. TB	Max TB	Time	CTM	Freezing point	Super-cooling limit	Source
				Gopherus agassizii			
30.6	19.0	37.8					Brattstrom, 1965
32.3	20.8	38.0	late May				McGinnis and Voigt, 1971
34.7	27.5	38.3	mid July				McGinnis and Voigt, 1971
					—0.95	—4.40	Lowe et al., 1971
				43.1			Hutchison et al., 1966
				Gopherus berlandieri			
31.1	24.1	35.6	Spring				Judd and Rose, 1977
33.1	28.0	39.0	Summer	43.7			Judd and Rose, 1977
				39.0-43.0			Brattstrom, 1965
				42.8			Hutchison et al., 1966
					—0.38	—5.25	Lowe et al., 1971
				Gopherus flavomarginatus			
30.8	19.5	38.0	Spring and				Overall
31.5	24.8	38.0	summer				Excluding basking
				Gopherus polyphemus			
34.7	31.7	38.3	June and				Douglass and Layne, 1978
	34.0	35.0	August				Bogert and Cowles, 1947

toises tested, and the corresponding increase in time (due to this size) to attain the preferred temperature for activity. One should expect that the hiatus between pre and post 1200 hrs TBs would be narrower (or eliminated) with smaller tortoises that could warm faster and with individuals inhabiting areas where pre-emergence TB is closer to TAsun. Nonetheless, the differences in mean TB before and after 1200 hrs, after the basking temperatures were removed from the calculations, indicate that time of day at which TBs were determined could influence the mean TB obtained.

Elaborate burrow construction is common to three of the four species of *Gopherus* (although some *G. polyphemus* do not do so, W. Auffenberg, personal communication). The burrows obviously aid individual *G. polyphemus* and *G. agassizii* during cold weather in the northern portions of their ranges, yet burrow construction is also maintained at lower latitudes were TA rarely reaches 0°. In addition, the current range of *G. flavomarginatus* is such that freezing temperatures would occur rarely. It would appear that the burrows provide a thermal shield that protects the tortoises from heat or cold stress. In addition, the burrows provide a primary escape channel of known location during basking, aid in retarding respiratory water loss during basking, provide protection from predators, and form a central focus of activity for certain behaviors such as egg-laying.

In summary, mean TBs of all four species of *Gopherus* appear to be similar (ranging from 30-35°). The long basking time for the large *G. flavomarginatus* accounts for the differences between morning and afternoon mean TBs, which also closely correlate with TAsun.

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IDENTIFICATION OF SEVEN SPECIES OF PEROMYSCUS FROM TRANS-PECOS TEXAS BY CHARACTERS OF THE LOWER JAWS

WALTER W. DALQUEST AND FREDERICK B. STANGL, JR.

Field parties from Midwestern State University recently obtained a large collection of mammal remains from Pleistocene and early Recent deposits in a cave in southern Culberson County, Texas. Identification of the remains of *Peromyscus* from the cave presented major problems because seven species of this genus occur in Culberson County today (Schmidly, 1977), and specimens of four species were trapped within a few hundred yards of the cave mouth. An eighth species, *Peromyscus crinitus,* is found in western New Mexico and has been reported from cave deposits in Eddy County, New Mexico, only 100 miles to the north.

Other workers have encountered this same problem. Harris (1974) listed five species of *Peromyscus* (including *P. crinitus*) from Dry Cave, Eddy Co., New Mexico. Logan and Black (1977), working with *Peromyscus* from Upper Sloth Cave, in northern Culberson County, Texas, referred upper molars lacking styles and lophs in the major valleys to *P. eremicus* and those of all other specimens to "*Peromyscus* sp." Lundelius (1977), who studied a collection of subfossil bones from Pratt Cave in northern Culberson County, referred jaws with large teeth to *P. difficilis* and those of all other specimens of the genus to "*Peromyscus* sp."

Because our collection from southern Culberson County included a quantity of relatively well-preserved lower jaws, we examined specimens of all species of Recent *Peromyscus* of concern to determine if characteristics of the lower jaws would permit identification on that basis alone.

In fossil *Peromyscus* jaws from cave deposits, mandibular rami are the bones most commonly found; coronoid and articular processes and the angle of the jaw often are broken away and some teeth frequently are missing. The third molar is most often lost and the first most often present. Characters normally of practical value, therefore, are those of the ramus (Fig. 1) and lower first molar (Fig. 2).

Because geographic variation is, or may be, marked in some of the characters used, we confined our work to Recent material from Trans-Pecos Texas and immediately adjacent areas in New Mexico. Whenever possible, we used specimens from Culberson County, but were forced to use some material from adjacent counties or even farther away. Only for *Peromyscus truei* and *P. difficilis* did we depend on specimens from New Mexico.

Some of the characters used could be detected only in teeth in slight to moderate stages of wear. Young specimens—those with more than a small amount of the gray or bluish immature pelage—were rejected, as were aged mice with the enamel pattern of m1 worn flat or nearly so. Field collectors often tend to save the large and brightly colored individuals taken in their traps, and this bias results in large numbers of old to senile individuals preserved in collections. We had to search the collections of Midwestern State University, Texas Tech University, and Texas A&M University to obtain adequate series of some species. In the case of *Peromyscus truei,* only four suitable animals were available. We found that dentitions of specimens of *P. truei* from farther west, within the main geographic range of the species, appeared markedly different in some respects from the four specimens from Texas and eastern New Mexico, the eastern extremity of the range. Therefore, we have listed our findings for these four individuals only.

Details of the enamel pattern of the first lower molar were determined using a dissecting microscope; all measurements were made with an ocular micrometer. Specimens were chosen from museum trays until an arbitrary number of 28 jaws at the proper stage of tooth wear were found. Sex of specimens was disregarded inasmuch as it cannot be determined from fossil jaws.

We found characters of major value to be as follows: the nature of the incisor-base capsule, alveolar length of the lower molar row, and details of the enamel pattern m1.

Incisor-base capsule.—The proximal end of the lower incisor in *Peromyscus* is enveloped in the permanent enamel-forming organ and dental epithelium. The organ lies at the level of the masseteric crest on the labial margin of the ramus. The bone swells slightly to greatly at this point to form a thin-walled, bony capsule containing the enamel-forming organ. We rated the capsule in three grades. In Grade O there is only a slight labial bulge at the site of the enamel-forming organ when the jaw is seen from directly above, with coronoid process and labial side of the jaw held on the same plane. In lateral view, the capsule is seen to rise only slighly to moderately above the masseteric crest, and only the dorsal outline of the capsule is distinct. The postero-dorsal margin merges imperceptibly with the jaw ramus. In Grade 1, the capsule makes a strong bulge when seen from above, and in lateral view both dorsal and posterior margins are well marked. The bone of the posterior margin is not recessed, however, and there is no true groove outlining the posterior margin. In Grade 2, the capsule is recessed on both dorsal and posterior margins, so that a blunt, fingerlike projection is formed; the masseteric crest is strongly distorted in lateral view.

Length of molar row.—Because some teeth often are lost in fossil *Peromyscus* jaws, we depended on the alveolar length of the toothrow. Measurements were taken on the lingual side, with the jaw slightly tilted, so that the margins of the alveoli were visible.

Length and breadth of first lower molar.—The m1 of *Peromyscus* is somewhat bulbous, reaching maximum diameter well below the top of the crown of the unworn tooth. When the tooth is worn below this level, measurements, especially of length, are deceptively small and become still smaller with additional wear. Maximum occlusal surface is exposed quite early in life, not long after the adult pelage is in place.

The first lower molar was viewed from the lingual side, perpendicular to the lingual surface of the ramus. If the anterior edge of m1 thus shown did not disclose an inward curve at the top, the maximum occlusal surface was not yet exposed and the specimen was rejected. In specimens of the proper age, measurements were taken from the anteriormost point of the anterior curvature of the tooth to the vertical line of contact with m2. Breadth of m1 was measured at the broadest point of the talonid.

Anteroconid of first lower molar.—Typically, the anteroconid of m1 of *Peromyscus* bears a slight notch or groove on the anterdorsal surface of the unworn tooth. This notch is often absent

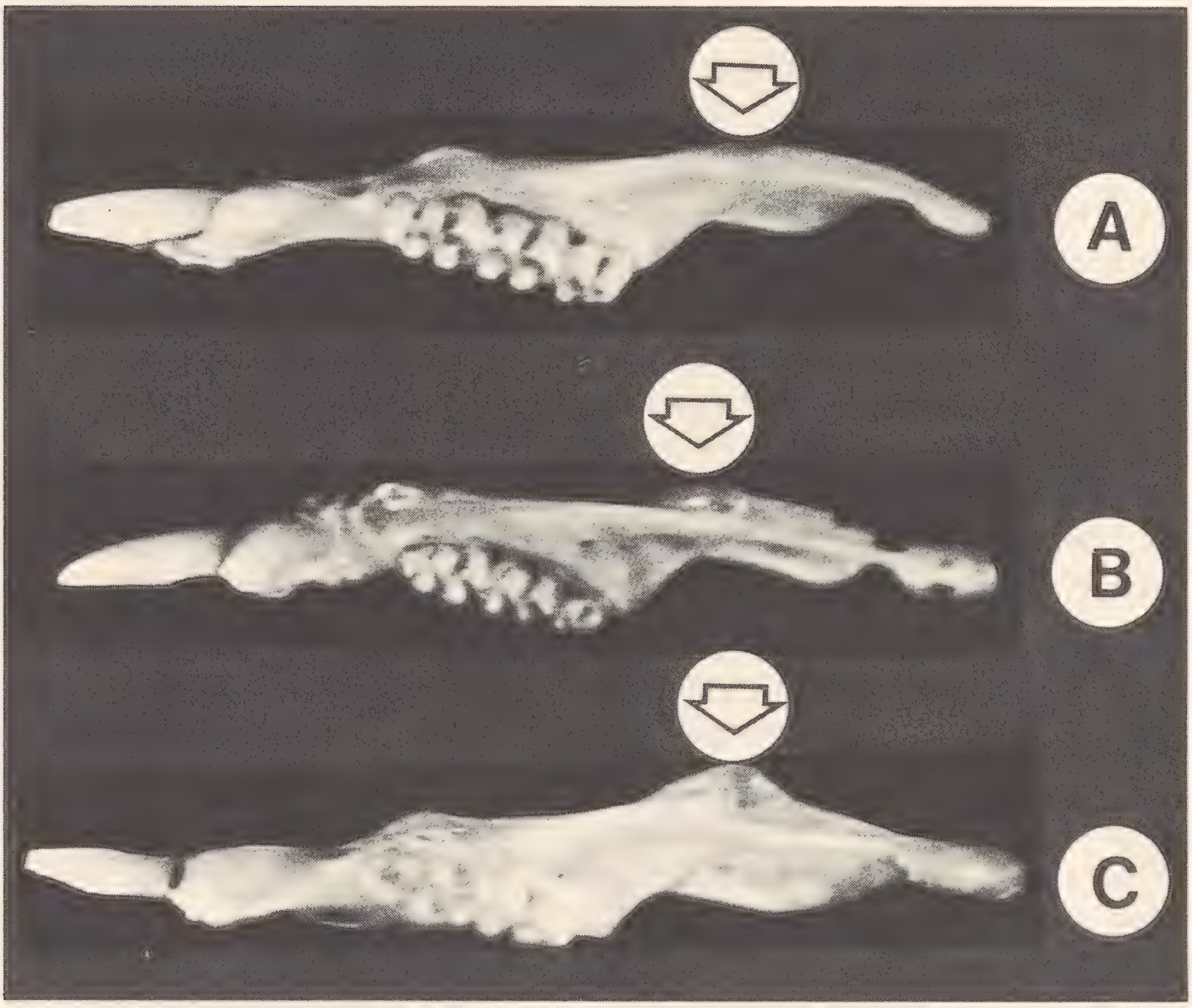

FIG. 1.—Dorsal view of *Peromyscus* jaws, displaying grades of bulge of the incisor-base capsule (arrows). A is Grade 0, B is Grade 1, and C is Grade 2.

and even when present, may be so shallow that it is worn away in early stages of attrition; this we consider Grade O. In some species the notch, though narrow, is persistent and moderately deep until rather late stages of moderate tooth wear; this is Grade 1. In Grade 1, the groove is so narrow that there is little or no space between the enamel surface. In Grade 2 there is a distinct valley separating the anteroconid into inner and outer parts. This valley, with the valley between anteroconid and metaconid, may give the trigonoid a trefoil or clover-leaf appearance.

Lophids and stylids.—Hooper (1957) made a detailed study of lophs, styles, lophids, and stylids in *Peromyscus*. This work involved structures of all teeth, including elevated structures visible only under high magnification. Cornely *et al.* (1981) treated the dental patterns of *Peromyscus* in their study of these mice in Guadalupe Mountains National Park, Culberson Co., Texas. We have confined our observations to the stylids and lophids blocking the two major valleys of the m1—ectosylid, mesostylid, ectolophid, and mesolophid.

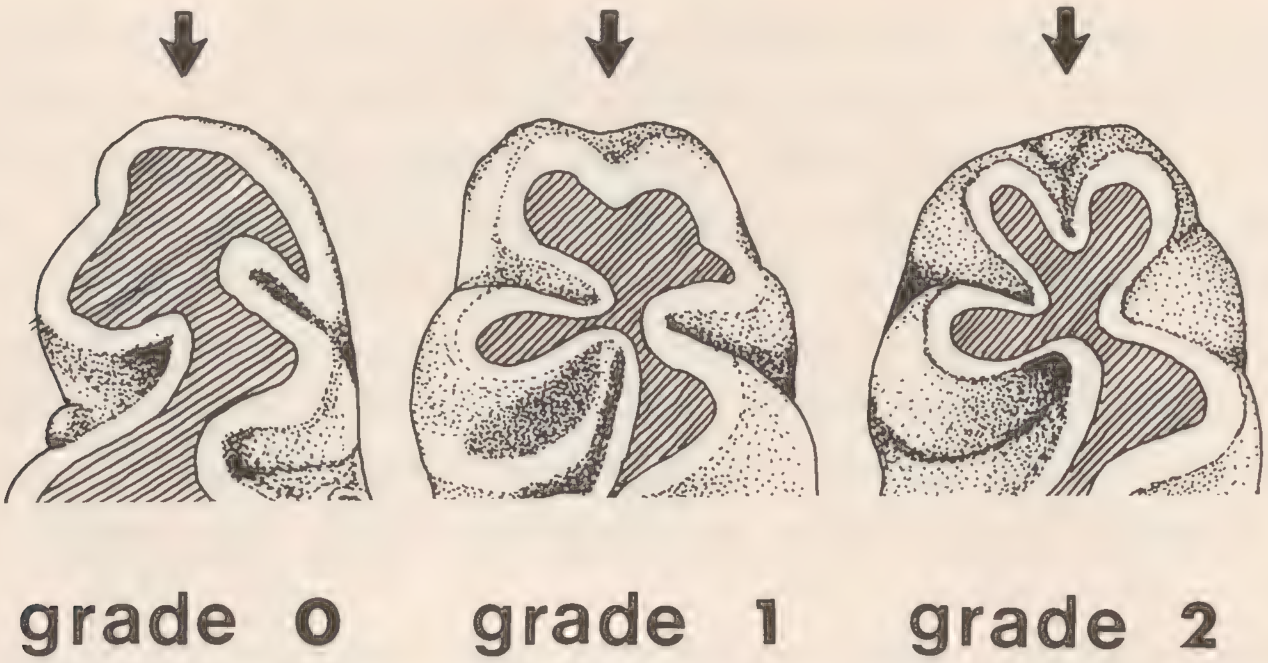

FIG. 2.—Dorsal view of occlusal surface of right lower m1 from *Peromyscus,* displaying grades of division of anteroconid (arrows).

We have counted as stylids only those cusps prominent enough to be seen in lateral view with a 10-power lens. We did not count the small projections or roughnesses that sometimes occur in the length of a valley, but only stylids that were large enough to block partially or completely the mouths of the valleys. A low but often sharp-edged cingulum sometimes closes the mouth of a valley. If this cingulum was level along its crest, it was not counted as a stylid, even if faint to moderate grooves separated the structure from the walls of adjacent cusps. If the structure was separated from the walls of adjacent cusps by distinct valleys, it was considered a stylid, even if it was not actually a pointed cusp. In most instances, however, stylids counted were conical structures with one distinct point or several closely grouped tiny points at the apex.

Lophids were counted if they were distinct enamel folds reaching out from the body of the tooth into a major valley, regardless of whether they were elevated to the level of the triturating surfaces of the tooth or lay at a lower level in the valley. Mere wrinkles and deflections of the enamel were not counted.

Lophids sometimes had a constricted area near the termination of the fold and thus might have been considered a lophid plus a stylid. In such cases, we counted only the lophid. More rarely a lophid had an elevated area on the crest of the fold and thus also might have been considered a lophid plus a stylid, although this would be obvious only in early stages of wear. We disregarded these accessory stylids also.

In our treatment, a major valley could have only one structure present—a stylid or a lophid. Thus, m1 might have the following possible combinations: neither stylids or lophids, one stylid, two stylids, one stylid and one lophid, one lophid, or two lophids.

Other characters.—Other characters showed some promise as criteria for identification of species and were considered, but are not documented here in detail. For example, multiplying length by breadth of m1 gave a crude approximation of the area of the occusal surface of the tooth. We did this for the seven species of *Peromyscus* from Culberson County, but the results obtained were essentially the same as obtained from the length of m1 alone.

Dalquest *et al.* (1969) found that the tendency to develop isolated lakes helped to separate *Peromyscus "boylii"* from *P. pectoralis* on the Edwards Plateau of Texas. The taxon considered *P. boylii* in that work has since been accorded full specific status as *P. attwateri* (Schmidly, 1973). The lower dentition of *P. attwateri* is extremely different from that of *P. boylii* from Trans-Pecos Texas. Development of isolated enamel lakes in the lower molars is not strong in the species of *Peromyscus* found in Southwestern Texas and is a transient feature, obvious only at later stages of wear. The lakes are rarely detectable in specimens as young as those used in this study.

Dalquest *et al.* (1969) also separated *Peromyscus maniculatus* from *P. leucopus* on the Edwards Plateau by the length of m1-m2. In the jaws from the cave in southern Culberson County, few individuals had both of these teeth present, so we did not study this feature.

The development of the third lower molar also may prove to be important in identification, but few of our fossil jaws contained this tooth.

CHARACTERIZATION

Tables 1 and 2 reveal that overlap in characters studied made it difficult to identify positively a single lower jaw to species in many instances. In most features, however, the overlap between some species was slight, resulting from one or two variant individuals. Given a large series of lower jaws of mixed species of *Peromyscus* from Trans-Pecos Texas, use of combinations of characters often made it possible to determine whether or not a species was present, to identify some individual jaws to species, and to narrow the identification of other jaws to one of two species. Fossils from late Pleistocene age cave deposits frequently include quantities of presumably mixed species of *Peromyscus*,

TABLE 1.—*Development of incisor-base capsule, division of anteroconid of first lower molar, and development of stylids and lophids in first lower molar of seven species of* Peromyscus *(N=28 except for* P. truei *where* N=4*).*

	maniculatus	*leucopus*	*eremicus*	*boylii*	*pectoralis*	*difficilis*	*truei*
Incisor capsule 0	0 (0%)	0 (0%)	11 (39%)	28 (100%)	28 (100%)	28 (100%)	4 (100%)
Incisor capsule 1	10 (36%)	1 (4%)	11 (39%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Incisor capsule 2	18 (64%)	27 (96%)	6 (21%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Anteroconid 0	22 (79%)	28 (100%)	23 (82%)	12 (43%)	1 (4%)	3 (11%)	2 (50%)
Anteroconid 1	6 (21%)	0 (0%)	5 (18%)	15 (54%)	10 (36%)	3 (11%)	1 (25%)
Anteroconid 2	0 (0%)	0 (0%)	0 (0%)	1 (4%)	17 (61%)	22 (79%)	1 (25%)
No stylids	24 (86%)	25 (89%)	14 (50%)	20 (71%)	4 (14%)	4 (14%)	3 (75%)
With stylids	4 (14%)	3 (11%)	14 (50%)	8 (29%)	24 (86%)	24 (86%)	1 (25%)
Ectostylids	1	1	5	6	9	3	1
Mesostylids	3	2	9	1	10	5	0
Total stylids	4	3	14	7	19	8	1
No lophids	26 (93%)	28 (100%)	20 (78%)	27 (96%)	5 (18%)	5 (18%)	3 (75%)
With lophids	2 (7%)	0 (0%)	8 (29%)	1 (4%)	23 (82%)	23 (82%)	1 (25%)
Ectolophids	1	0	7	1	17	20	1
Mesolophids	1	1	3	0	11	19	0
Total lophids	2	1	10	1	28	39	1

TABLE 2.—*Measurements (mm.) of lower dentition in seven species of* Peromyscus.

	maniculatus (*N*=28)	*leucopus* (*N*=28)	*eremicus* (*N*=28)	*boylii* (*N*=28)	*pectoralis* (*N*=28)	*difficilis* (*N*=28)	*truei* (*N*=28)
			Length m1-m3				
Minimum	3.42	3.55	3.55	3.65	3.65	4.10	3.85
Maximum	4.00	4.15	3.95	4.20	4.10	4.70	4.20
Mean	3.74	3.87	3.72	3.93	3.89	4.36	4.05
SD	0.14	0.18	0.13	0.12	0.12	0.14	0.16
			Length m1				
Minimum	1.40	1.50	1.50	1.65	1.65	1.85	1.75
Maximum	1.75	1.85	1.75	1.85	1.85	2.05	1.85
Mean	1.63	1.66	1.61	1.73	1.71	1.94	1.80
SD	0.09	0.08	0.07	0.05	0.05	0.06	0.06
			Breadth m1				
Minimum	0.90	1.00	0.90	1.00	0.95	1.10	1.05
Maximum	1.15	1.10	1.10	1.10	1.15	1.35	1.10
Mean	1.01	1.03	1.10	1.06	1.04	1.17	1.08
SD	0.06	0.03	0.04	0.03	0.05	0.06	0.05

and any means of separating the collection may yield important information as to past distribution, paleoecology, and climatic conditions at the collecting sites. The data here assembled permit characterization of the species studied as follows.

Peromyscus maniculatus.—Incisor-base capsule always strongly to moderately well developed; anteroconid usually not divided (79% Grade 0); stylids and lophids uncommon to rare (14% and 7%, respectively).

Peromyscus leucopus.—Incisor-base capsule always strongly developed; anteroconid almost never divided; stylids uncommon (11%) and lophids absent.

Peromyscus eremicus.—Extremely variable; incisor-base capsule Grade 0 in about a third (39%) of the series; anteroconid usually not divided (82%) and if divided not strongly so; stylids present in about half of the first lower molars, lophids present in about a third (29%).

Peromyscus boylii.—Incisor-base capsule always Grade 0; anteroconid divided in about half the jaws, but usually not deeply so; stylids present in about a third (29%) of the jaws but lophids usually absent.

Peromyscus pectoralis.—Incisor-base capsule always Grade 0; anteroconid almost always divided, usually deeply so; stylids and lophids usually present (86% and 82%).

Peromyscus difficilis.—Size large, alveolar length of m1-m3 greater than 4.1 mm.; incisor-base capsule always Grade 0; anteroconid usually divided (90%); stylids and lophids usually present (86% and 82).

Peromyscus truei.—The following is based on only four specimens. Mice examined from Arizona and westward had teeth so different from those of the four individuals from the eastern edge of the geographic range of this species that we did not include them in the study. Size larger than all species except *P. difficilis;* incisor-base capsule Grade O; anteroconid divided in half the jaws; stylids and lophids each present 25 per cent of the time.

Peromyscus crinitus.—This species is not included in the tables because we have no evidence that it ever occurred in Texas, although it is found today as far as the western-central border of New Mexico and Harris (1974) included *P. crinitus* in the fauna from Dry Cave, Eddy County, in that state. His listing is queried, but apparently on chronologic rather than taxonomic grounds. This is a distinctive species, as seen from specimens examined from Arizona and Utah. Size small, alveolar length of m1-m3 3.0 to 3.5 mm.; incisor-base capsule strongly developed but small in diameter; anteroconid not divided; stylids and lophids absent. One is more apt to confuse a lower jaw of this mouse with one of *Reithrodontomys* rather than with that of another species of *Peromyscus.*

IDENTIFICATION

The strongly developed incisor-base capsule serves to separate *Peromyscus maniculatus* and *P. leucopus* from all other Trans-Pecos members of the genus except *P. eremicus. P. eremicus* had a well-developed capsule in more than two-thirds of the specimens examined. *P. leucopus* averages larger than *P. maniculatus* and *P. eremicus,* but there is broad overlap in the alveolar length of m1-m3. A character helpful in separating *P. leucopus* from *P. maniculatus* and *P. eremicus* is the size of the occlusal surface of the anteroconid. In *P. leucopus,* the surface is usually a large, broad, tilted plane extending back to the metaconid and protoconid. In the other two species, it is usually smaller and narrower. Although readily apparent to the eye, this feature is difficult to measure. The absence of lophids in the m1 of *P. leucopus* is also helpful. A jaw with a well-developed incisor-base capsule and with lophids might be *P. maniculatus* or *P. eremicus* but not *P. leucopus.* If a lophid and a stylid are present in m1, the jaw is probably *P. eremicus.* Although most *P. leucopus* and some *P. eremicus* can be selected using characters mentioned above, many specimens, probably including most of the *P. maniculatus,* cannot be positively identified.

Hooper (1957), in his detailed studies of the accessory structures in *Peromyscus* molars, commented on the simplicity of the teeth of *P. eremicus.* This alleged simplicity (absence of lophs, stylids, lophids, stylids) has been mentioned by later writers, and even used as a key character in identification. However, Hooper's remarks were not intended to be thus taken. His tables and figures show that accessory structures do occur in *P. eremicus,* that they vary geographically, and that they are more common in Texas than to the west and south. We found that in Trans-Pecos Texas stylids occur in about half of the lower first molars of *P. eremicus* and lophids in almost a third. On the other hand, *P. leucopus,* shown by Hooper (1957) to have moderately complicated teeth in parts of its geographic range, has extremely simple teeth in Trans-Pecos Texas.

Of the jaws lacking the well-developed incisor-base capsule, *Peromyscus difficilis* is identifiable by extreme alveolar length of m1-m3 (greater than 4.1 mm.) and by a deeply divided anteroconid and presence of stylids and lophids on m1. It is possible, however, that some large *P. truei* might be difficult to separate from small *P. difficilis.*

Peromyscus pectoralis and *P. boylii* are similar in size. In Texas, these species are sometimes sympatric and, were it not for the dark ankles of *P. boylii* and white ankles of *P. pectoralis,* freshly taken individuals would be difficult to separate. The lower m1 is diagnostic, however, because *P. pectoralis* has a deeply divided anteroconid, and stylids or lophids (or both) are almost invariably present. In *P. boylii,* the enamel pattern is simple—the anteroconid divided only about half of the time, stylids uncommon, and lophids almost always absent.

Those *Peromyscus eremicus* that lack the well-developed incisor-base capsule (less than one-third of the individuals examined) may be difficult to separate from *P. pectoralis* and *P. truei. P. eremicus* is smaller (jaws with alveolar length of m1-m3 greater than 3.95 mm. would not be *eremicus*), the anteroconid when divided is not deeply so (thus contracting with 60% of *P. perctoralis* teeth), and lophids are commonly present (20% as contrasted with only 4% in *P. boylii).*

General Application

We compared species from Trans-Pecos Texas with specimens of the relevent species from various localities in the United States and Mexico. Some of the characters, such as the nature of the incisor-base capsule have broad application. Other characters may be subject to considerable geographic variation, although most (except in *Peromyscus eremicus*) are relatively stable in any geographic area. Before the characters here discussed can be applied to a collection of jaws of mixed species of *Peromyscus,* the characteristics of those taxa occurring at or near the collecting site should be ascertained.

Features that serve to separate species in one area may or may not do so elsewhere. For example, we found that *Peromyscus maniculatus blandus* from Trans-Pecos Texas averaged smaller than *P. leucopus tornillo* from the same area, but measurements overlapped so broadly that alveolar length of m1-m3 was of little value in separating the two. In contrast, there is a broad zone in central Texas where *P. m. pallescens,* a diminutive race, occurs together with *P. l. texanus,* a robust-bodied race. In this area, the two species can be separated by size alone.

Culberson County, Texas, where any of eight species of *Peromyscus* could occur in a late Pleistocene fauna, is a special case. Our study reveals that identification would be greatly simplified in a collection of jaws from a locality where *P. eremicus* is not expected.

Properly used, the lower jaw ramus and first lower molar are of value in identifying specimens of *Peromyscus* to species, but only when used with care. Some of the *Peromyscus* jaws from later Pleistocene deposits that are identifed to species in the literature should be accepted only with caution.

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